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ERRATA

"Studies on Contact Insecticides, Part III," by TATTERSFIELD, GIMINGHAM, AND MORRIS.

p. 231. *Read* Guaiacol *for* Guiacol.

pp. 242, 246–248. Heading of column 7. *Read* "% not hatching" *for* "% hatching."

p. 244. Diagrams 9 and 10. *Read* "Percentage eggs killed" *for* "Percentage moribund and dead."

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STUDIES IN CACAO

PART I. THE METHOD OF POLLINATION

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Introduction.

INVESTIGATIONS on the pollination of the cacao flower have so far yielded no definite results. The structure of the flower with the characteristic hooded petals enclosing the stamens, favours neither self- nor cross-pollination, though there is considerable evidence from various sources that natural crossing occurs to a considerable extent. The opinions of various observers on the method of pollination may be briefly summarised.

Knuth (4) saw a bee (*Apis mellifica* L.) as a visitor of cacao flowers in Java. According to Wright (1907) (7) Dr Uzel carried out experiments in Ceylon and concluded that the flowers were pollinated by thrips. Wright also mentions that Green has recorded in Ceylon the occurrence of 30 specimens of a common aphis (*Ceylonica theaecola* Buckt) in a cacao flower, each being dusted with numerous pollen grains. Winkler, cited by Hunger (1922) (2), expresses the opinion that pollination is effected by ants which always occur plentifully on cacao trees. According to von Faber (van Hall, 1914 (6)) the flowers were chiefly self-pollinated. He says:

> Though the structure of the flower seems to eliminate the possibility of self-pollination, this is really not so. The long and supple flower stalk facilitates the swinging to and fro of the hanging flower by the wind. Experiments proved that by this movement pollen falls easily from the anthers on the pistil of the same flower, and it could be demonstrated that isolated flowers were easily self-pollinated in this way. Self-pollination may therefore be regarded to be the rule in the cacao flower. When, however, neighbouring trees stand close to each other it is also possible that pollen falls from the hanging blossoms and settles on the pistil of flowers on the neighbouring tree. In this way, cross-fertilisation is possible when the trees stand in close proximity.

Hart (1911) (1) states that he worked on the question of cacao pollination in Trinidad, and inferred that pollination is effected by means of several kinds of minute insects.

Jones (1912) (3) carried out a series of experiments in Dominica which, although inconclusive, constitute the best work which has so far been done on the subject, though his paper is not mentioned either by van Hall or by Hunger. He examined a large number of flowers for presence of pollen on the stigma and noted that only two flowers out of 137 showed any pollen. This is in accordance with van Hall's observation that of 299 flowers only 13 were pollinated. Jones enclosed several groups of flowers in muslin cages, and in no case found pollinated flowers. He concluded that pollination could not be effected without outside agency. His next series of experiments was with flowers which had a number of small insects on the stems, presumably aphis attended by ants. Excluding ants by means of muslin cages he failed to find evidence of pollination, while microscopic examination of insects found in cacao flowers did not reveal the presence of pollen on their bodies. He therefore formed the opinion that in Dominica these small insects have little if any direct power of causing pollination, and finally concluded that the flowers are largely pollinated by ants, which are attracted to the flower by aphides, and in the process of nursing these insects come into contact with the pollen and transfer it to the stigma.

Reviewing the above evidence, the general opinion is that small insects, either ants, aphides, thrips, or a combination of all three, are the chief agents concerned in the pollination of the cacao flower. Von Faber's view that the shaking of the flower by the wind causes self-pollination is probably incorrect, though van Hall (*loc. cit.*) says that his investigations "solved the question." A series of experiments carried out by the writer in which flowers were subjected to violent shaking to imitate the action of the wind gave negative results, the sole effect being to dislodge a certain amount of pollen from the anthers into the petaloid hoods. No pollen could ever be detected on the stigmas whether the shaking was gentle or violent, brief or prolonged.

Direct proof of natural crossing.

A peculiar type of cacao tree occurs in small numbers on plantations in Trinidad. It is known as "male cacao," and is so called because it produces pods which though small are normal, yet contain no seeds. Examination of flowers of this type of tree revealed a condition of complete male sterility—the anthers never containing pollen. Examination of stigmas showed that of 100 flowers, 9 had varying amounts of pollen. Without going further then, the transference of pollen from tree to tree by some outside agency is directly proved.

THE PART PLAYED IN POLLINATION BY RED ANTS AND APHIDES.

Examination of a large number of flowers showed that a varying proportion had numbers of aphides on the petioles and that these were invariably attended by red ants. In some cases microscopic examination revealed sporadic pollen grains sticking to the bodies of the aphides. It was clear that aphides and ants often wandered about the inside of the flower, and a single case was seen of an aphis with pollen grains sticking to it, walking over the stigma of the flower. The impossibility of establishing by direct observation the part played by ants and aphides in pollination, led to a series of experiments in which the life histories of three sets of flowers were recorded daily:

1. Flowers attended by ants and aphides.
2. Flowers artificially pollinated.
3. Flowers not attended by ants and aphides (controls).

The results are presented in Tables I–III below:

Table I.

A = Aphides and ants present.
B = Controls.

No. of exp.	No. of observations	Type of flower	No. of flowers remaining after following no. of days: 1	2	3	4	5	6	7	8	9	10	% set
1	101	A	19	10	9	3	3	3	3	3	3	3	3·0
	101	B	20	9	7	6	5	4	3	3	3	3	3·0
2	109	A	42	24	16	10	6	5	3	2	2	2	1·8
	109	B	17	8	5	2	1	0	0	0	0	0	0·0
3	102	A	23	15	7	6	5	2	2	1	1	0	0·0
	102	B	8	4	2	0	0	0	0	0	0	0	0·0
4	106	A	23	16	11	8	7	5	2	1	1	1	0·9
	106	B	7	3	0	0	0	0	0	0	0	0	0·0
5	103	A	29	16	9	7	4	4	3	2	2	1	1·0
	103	B	10	3	1	0	0	0	0	0	0	0	0·0
6	105	A	20	10	6	5	2	2	2	2	2	2	1·9
	105	B	8	2	1	1	1	1	1	1	1	1	0·9
7	106	A	20	17	14	9	7	2	2	2	2	2	1·9
	106	B	4	2	1	0	0	0	0	0	0	0	0·0
Total	732	A	176	108	72	48	34	23	17	13	13	11	1·50
	732	B	74	31	17	9	7	5	4	4	4	4	0·55

Table II.

Comparison of the rate of shedding of pollinated and unpollinated flowers.

B = Controls.
C = Pollinated.

No. of exp.	No. of observa-tions	Type of flower	No. of flowers remaining after following no. of days										% set
			1	2	3	4	5	6	7	8	9	10	
8	115	B	21	11	5	3	1	0	0	0	0	0	0·0
	115	C	63	58	50	38	27	21	17	17	16	15	13·04
9	89	B	8	5	2	0	0	0	0	0	0	0	0·0
	89	C	40	34	24	23	10	5	5	5	5	5	5·6
10	109	B	14	2	2	0	0	0	0	0	0	0	0·0
	218	C	131	120	98	70	45	35	27	23	20	20	9·1
11	111	B	15	2	0	0	0	0	0	0	0	0	0·0
	222	C	112	105	92	63	38	24	17	17	16	15	6·7
12	112	B	5	2	0	0	0	0	0	0	0	0	0·0
	224	C	103	83	72	50	27	9	7	4	1	1	0·44
13	113	B	14	6	4	4	3	3	1	1	1	1	0·88
	226	C	102	80	66	41	19	13	9	8	8	7	3·09
14	102	B	8	3	3	2	1	1	0	0	0	0	0·0
	204	C	58	45	36	23	13	8	7	7	5	5	2·4
15	220	B	19	7	2	0	0	0	0	0	0	0	0·0
	220	C	74	54	36	24	18	14	12	9	9	9	4·09
Total	971	B	104	38	18	9	5	4	1	1	1	1	0·10
	1518	C	683	579	474	332	197	129	101	90	80	77	5·07

Table III.

Comparison of the rate of shedding of A, flowers with ants and aphides; B, controls; C, pollinated flowers.

No. of exp.	No. of observa-tions	Type of flower	No. of flowers remaining after following no. of days										% set
			1	2	3	4	5	6	7	8	9	10	
16	172	C	71	50	36	24	17	14	10	10	10	10	5·8
	172	A	43	30	19	13	9	8	5	5	5	5	2·9
	172	B	12	6	2	1	0	0	0	0	0	0	0·0

The main features of these Tables are as follow:

1. In flowers which have been adequately pollinated there is a survival of about 5 per cent. by the 10th day, at which time small fruits have developed of some 2–3 mm. diameter. After this time there is practically no further loss by abscission, though many fruits fail to reach maturity through a variety of causes. Pod rot due to *Phytophthora*

probably accounts for most of the loss. An important point for which at present no explanation can be given is that the rate of loss in the fully pollinated series is logarithmic.

2. In unpollinated flowers the number of pods finally set is about 0·3 per cent., while 90 per cent. of the flowers invariably drop in 24 hours.

3. In flowers attended by ants and aphides about 2 per cent. of setting occurs, and the curve of loss is intermediate between those of fully and unpollinated flowers. The curves for individual experiments show that in every case but one there is a less rapid reduction in the number of flowers in those attended by insects than in the controls. The difference in setting percentage is statistically significant, the odds being over 600 to 1 that ants and aphides cause a greater setting of fruit than the controls.

4. Direct observations on the number of flowers actually showing pollen on the stigma show that only about 5 per cent. ever receive any pollen at all. By calculation from the summarised data it may be concluded that thorough pollination takes place in about 35 per cent. of flowers attended by ants and aphides, and in 6 per cent. of the controls. No exact estimates of the number of flowers normally attended by ants and aphides have been made but it is certainly not more than 10 per cent.

DISCUSSION.

It is demonstrated by these experiments that the majority of cacao flowers pass through their life-history without adequate pollination, and confirmation is thus provided of previous observations by van Hall and Jones. The efficiency of pollinating agents probably varies considerably in different countries, since Lock (1904) (5) states that 50 per cent. of the flowers he examined in Ceylon showed more or less pollen on the stigmas, and therefore concluded that failure to set fruit was not due to lack of pollen. It is conceivable that lack of pollen may, under certain environmental conditions, act as a limiting factor in crop production, and further observations on the factors which influence the number of aphides are required. It may be suggested that more efficient pollination is likely to be found on the South American mainland, where cacao is indigenous.

The results of flower examination, involving the recording of the history of nearly 4500 flowers establish beyond reasonable doubt that either ants or aphides or both these insects are responsible for a considerable amount of pollination, on the site of the experiments, and the low percentage of setting on the controls renders it likely that they

constitute the chief pollinating agents. It is conceivable that thrips of the flower-inhabiting type also play some rôle, but they were practically absent in the material worked with.

The elimination of crawling insects in relation to pollination.

Having established the fact that crawling insects play some part in cacao pollination, an experiment was carried out in which all crawling insects were excluded from a flower-bearing section of the trunk of a single tree. A section of some 2 feet wide was isolated by two broad bands of a sticky mixture of resin, paraffin wax, and tar. All open flowers were removed and a thorough spraying given with kerosene emulsion in order to remove any crawling insects. Close examination of the trunk the following morning showed that no crawling insects were present. The stigmas of 97 flowers were examined, of which 95 showed no sign of pollen. Of the other two, one showed a large mass of pollen on the stigma, and the other a few grains. This pollen must have been conveyed by some flying insect, and probably one which is active during the night, since the flowers open in the early morning and the above examination was conducted at 8 a.m. A large number of flowers from the unbanded part of the trunk was subsequently examined, and one other flower was found with a similar mass of pollen on the stigma. These observations must be regarded as demonstrating the pollen-carrying activity of some unknown flying insect, but although its nature cannot at present be conjectured, it is relatively inefficient in the cacao plot where these experiments have been conducted. It is possible that it is more abundant at certain periods of the year, and its true status as a pollinating agent has still to be determined.

Summary.

1. Previous investigations on the pollination of cacao are reviewed. It is pointed out that the consensus of opinion is in favour of the pollinating agent being small insects, either thrips, aphides or ants.

2. Direct proof of natural crossing was obtained by examination of flowers on a male sterile tree, in which 9 per cent. of the flowers were found to be pollinated.

3. Daily examination of flowers artificially pollinated, flowers attended by ants and aphides, and flowers with no attendant insects, indicated that the majority of cacao flowers are never pollinated under Trinidad conditions. Adequate pollination took place in 35 per cent. of flowers attended by ants and aphides, and in only 6 per cent. of the

controls. It is concluded that ants and aphides are the chief pollinating agents in the field under examination.

4. Elimination of crawling insects demonstrated the presence of another pollinating agent, probably a night flying insect which pollinated about 1 per cent. of flowers.

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GROWTH AND CORRELATION IN THE OIL-PALM (*ELAEIS GUINEENSIS*)

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(With 3 Text-figures.)

The object of the work reported in this paper was to obtain information on the growth processes of the oil-palm (*Elaeis guineensis*). It was thought that such information might prove of value in formulating and interpreting the results of field experiments. Though tree records were initiated in 1922, yet the more intensive observations, with which the present communication is mainly concerned, were not undertaken until July, 1923. It will be evident that conclusions drawn from a study made over so short a period must be of an essentially tentative nature.

Description of Tree.

A brief description of the oil-palm may assist in rendering the scope of the work intelligible. The stem, which may attain a height of 70 feet, is crowned by 20–40 pinnate leaves, the latter emerging in whorls of three from the centre of the crown. When the pinnae are unfolded the leaves gradually arch outwards. The bases of the petioles of the young leaves form a coherent cylinder held together by a mass of intercrossing fibres. When the basal part of the petiole departs from this central cylinder the young spadix can normally be detected in the leaf axil. It is probably never absent though not infrequently it aborts before anthesis. As soon as the leaf arches outwards, the spadix can begin more active growth. After a very variable interval the spathe opens and anthesis ensues. The trees are usually monoecious, and the inflorescences, which are normally either male or female, tend to mature at different times, the latter developing into the bunches of fruit.

Plan of Work.

The population under observation consisted of 77 trees growing on the Moor Plantation, which is situated about 3 miles west of the town of Ibadan. The country round is thickly studded with oil-palms, but

their growth is less luxuriant than that which obtains in the more humid forest regions further south. The trees were planted in 1913 and were thus about 10 years old when the observations commenced. The distance of planting was 20 feet, and by 1923 a fairly complete canopy of leaves had been formed throughout the plot. It was evident that considerable foliar interference was occurring, but it is probable that the competition for light was not so severe as that obtaining under natural conditions elsewhere.

The following observations were made twice a week on each of the 77 trees:

(1) *Leaves.* The appearance of leaves was recorded as soon as the pinnae began to unfold.

(2) *Immature spadices.* Their presence was observed by placing the hand between the base of the petiole and the central cylinder of the petiole bases. The separation of the leaf base from the central cylinder probably does not represent any critical stage in the development of the spadix, except that prior to this its growth would be mechanically impeded.

(3) *Mature inflorescence.* The number and sex of the inflorescences was noted at anthesis.

Records were also kept of the following environmental factors: (1) rainfall, (2) evaporation from standardised spherical white Livingston atmometers, which were run in triplicate, and (3) sunshine on a Campbell-Stokes sunshine recorder.

General Growth Relations.

Fig. 1 illustrates the seasonal changes which occurred in the production of leaves and inflorescences in the population as a whole, and the extent to which these changes may be attributed to environmental factors. Considering first the distribution of rainfall, the months of December, January and February are normally characterised by drought, the rains usually commencing in March and continuing till November. The dry season of 1924, however, was more protracted than usual. Frequently there is a break in the rains about August but the annual variation in this respect is considerable. During this part of the year the sky is overcast nearly the whole day, and it is interesting to note that the break in the rains, even when marked, is without effect on atmospheric humidity. The curves of evaporation and sunshine both attain their maximum during the dry season and gradually decline on the approach of the rains.

Reverting now to the plant characters under review, it will be seen (Fig. 1) that changes in the rate of leaf production exhibit a close corre-

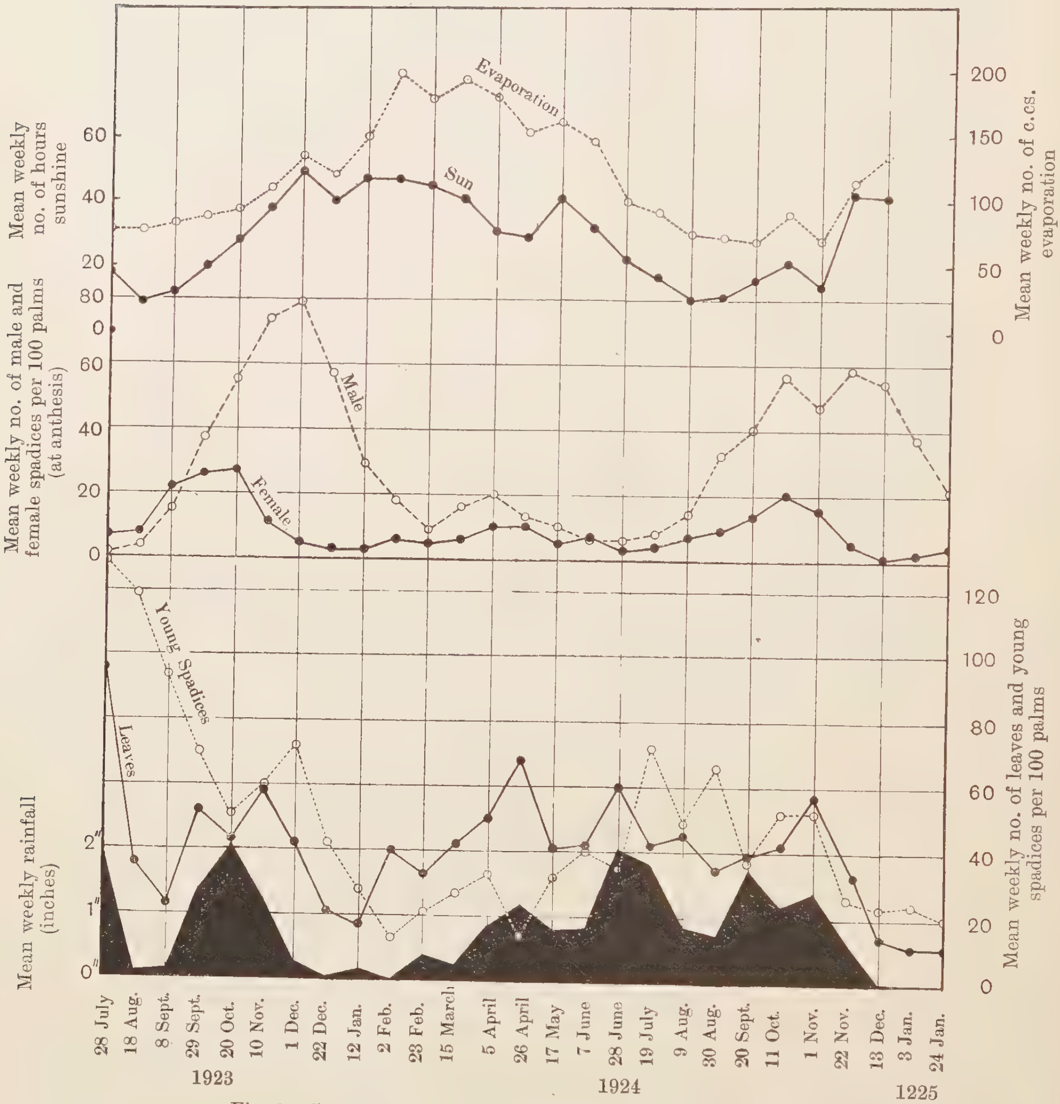

Fig. 1. General growth relations and environmental factors.

spondence with those of rainfall. However, in 1924 leaf production became augmented before the advent of appreciable precipitation. It seems probable that the acceleration in the rate of leaf production before

the termination of the dry season was due, in this case, to a release of assimilates, as the fruits set the previous September and October approached maturity. The drain on the plant's supply of assimilates as a result of the development of fruits in dry weather must be considerable, and is doubtless a factor retarding the production of leaves.

It will be noticed that the leaf production curve is followed some 3–6 weeks later by that of the young spadices. From this it will be gathered that the appearance of young leaves in the centre of the crown is followed some 3–6 weeks later by a tendency on the part of more mature leaves to separate from the central cylinder of leaf bases and to arch outwards, thereby permitting the detection of a young inflorescence in each axil. Their separation of course removes any mechanical impediment to the growth of the spadix. It is important to note that there is apparently one cycle of leaf production in the course of the year and one cycle of young inflorescences, but that both proceed very irregularly and follow generally the distribution of rainfall.

It will be noticed that there is but little similarity between the curves for male and female inflorescences at anthesis and that of the young inflorescences. The former are of a much more regular nature and show two cycles in the course of the year. The greater of these two cycles occurs in the autumn and the lesser in the spring. It will be observed that the number of male inflorescences greatly exceeds that of the female. It is by no means easy to assign a reason for the presence of two flowering cycles in the course of the year. The occurrence of two dry seasons, a short one about August and a longer one from December to February, naturally presents itself as a possible cause, but as its absence in August, 1924, failed to affect the flowering of inflorescences (Fig. 1) in the succeeding autumn, it appears that the cause must be sought elsewhere.

The relative length of day and night, a factor of much importance in initiating the reproductive processes in many plants (1, 2) even in the tropics (3) might conceivably, it seems, play a part in causing the double cycle of flowering. Fig. 2 illustrates the periodicity in the anthesis of female inflorescences in the population over a period of three years. The data were obtained by taking the number of bunches of fruits harvested monthly and antedating the whole series five months. This procedure has been adopted since the period between the flowering of the female spadix and the maturation of the fruits is approximately five months. It will be observed that the modes of the curve tend to synchronise with the periods of equal day and night. This tendency to

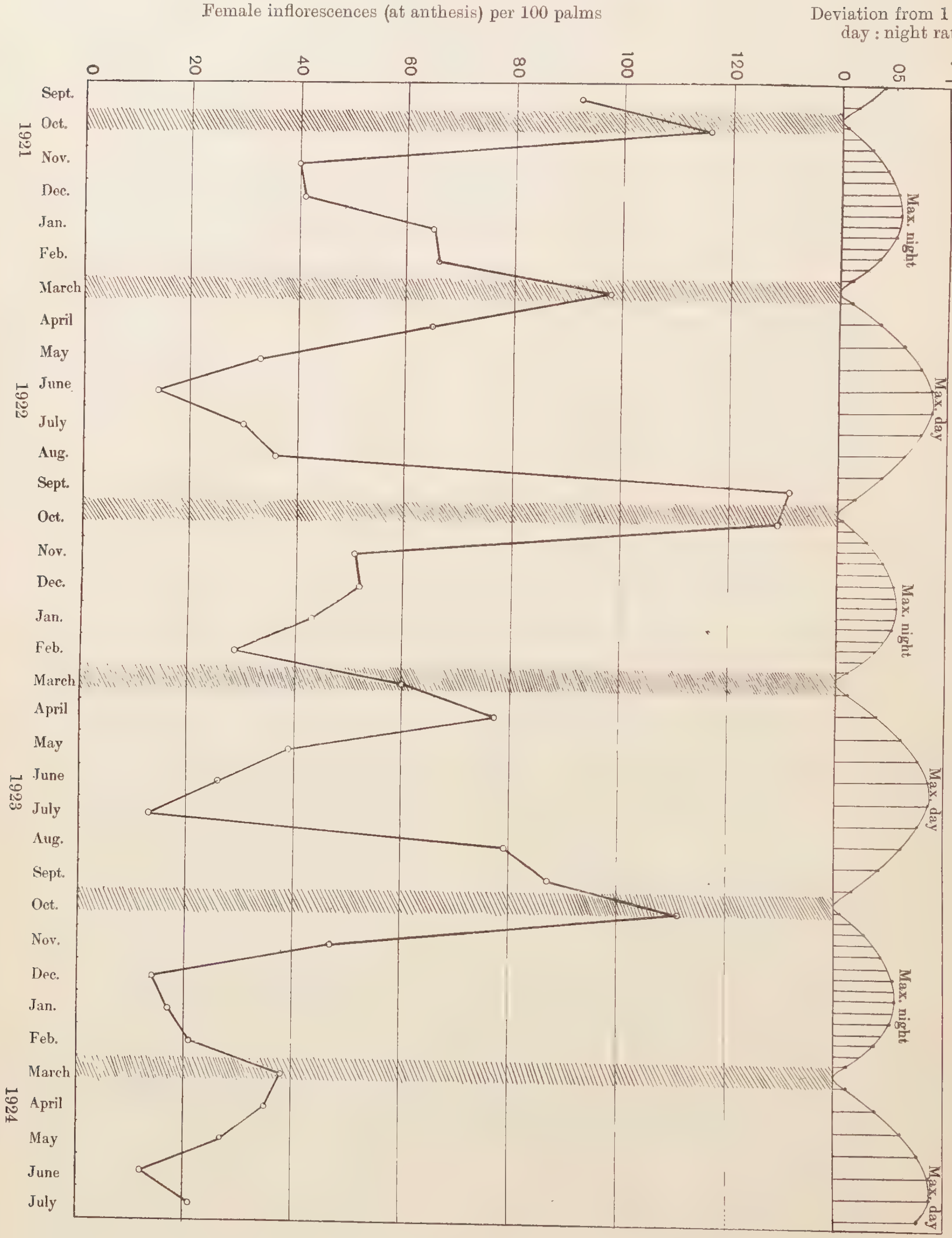

Fig. 2. The relation of the Spring and Autumn flowering cycles to the day : night ratio.

synchronisation is remarkable in view of the latitude of Ibadan (7° 22′ 30″), where the divergences from the 12-hour day are extremely small, the maximum and minimum days being 12 hrs. 30 mins. and 11 hrs. 40 mins. respectively. The greater of these flowering cycles occurs in autumn following the period of maximum day, while the lesser follows the period of maximum night. A similar phenomenon has already been recorded in the tropics (3). Although the difference in magnitude of the two flowering cycles is probably mainly due to other causes, it is possible that the ratio of day to night during preceding months may be a subsidiary factor.

An alternative explanation is to be found in the periodicity in leaf production; a periodicity, it will be remembered, that owes its origin to the distribution of rainfall. It is conceivable that there may be only one cycle of flowering following a single cycle of leaf production, but that the flowering cycle is interrupted by drought. This break would, of course, be enhanced by the strain of maturing fruits during the driest part of the year. Many young inflorescences would abort long before anthesis, especially if the dry season were unduly protracted or the crop of fruits set in the autumn were very heavy; no less than 45 per cent. of the immature inflorescences recorded in November, 1923, failed to achieve anthesis, whereas only about 2 per cent. of those recorded as present in the preceding August aborted. The chief objection to this view of the two flowering cycles lies in the fact that the March cycle of 1924 was preceded by an increase in the rate of leaf production and that many of the inflorescences that flowered at this time are to be traced to this activity in leaf production.

It would seem that no single explanation is entirely satisfactory. It may be necessary therefore to assume that one group of factors influences the laying down of the spadix primordia and that another group is concerned with their flowering. Whatever promotes leaf production will presumably accelerate the laying down of the primordia. Of the factors especially concerned with the flowering of the spadix the relative length of day and night is conceivably the most important.

THE ANNUAL DISTRIBUTION OF FEMALE INFLORESCENCES IN OLD AND YOUNG TREES.

From the economic point of view the periodicity in the production of bunches of fruits, which is determined of course by the flowering of female spadices some five months previously, is a matter of some importance. Not only is the March flowering cycle smaller than the

September one, but there is a tendency for it to diminish in magnitude in the three years under consideration (Fig. 2). It is patent that no decision as to the significance of this decrease is obtainable from records extending over so short a period, but fortunately the problem can be approached in another way.

Table I.

Showing Age as a factor in suppressing the Spring Flowering Cycle.

Height in feet	% of annual total female spadices flowering from Jan. to June (spring cycle)	Mean weight of bunches (lbs.)	Mean total weight of bunches for the year (lbs.)	No. of palms
1–10	47	9	23	13
11–20	45	18	67	11
21–30	40	28	109	15
31–40	26	26	130	22
41–50	28	24	134	29
51–60	21	22	115	12

Growing in a ravine on the Moor Plantation there is a group of oil-palms varying in size from seedlings to trees of more than 60 feet. In Table I these trees have been classed according to their height, and the percentage of the total number of female inflorescences produced in 1924 that flowered from January to June inclusive, has been calculated for each group. Inspection of the table will make it clear that as trees increase in height, and therefore in age, the spring flowering cycle tends to be suppressed. Caution must be exercised in drawing conclusions from a mixed population of trees of all sizes, for there will be a tendency for smaller individuals to suffer from competition with the larger ones. When considered, however, in conjunction with the results shown in Fig. 2 it seems probable that old trees tend to suppress the spring flowering cycle. Its disappearance may be due to the strain on the supply of reserve materials experienced by old trees in the maturation of their fruits, for the weight of the individual bunches seems to increase considerably as the trees mature. After the palm has attained a height of about 30 feet, however, the weight of the bunch does not apparently undergo any marked increase. The continued tendency for trees of over 30 feet to eliminate the spring cycle must therefore be due to other causes. Possibly the exhaustion of reserves becomes more pronounced with the onset of senescence.

INDIVIDUAL VARIABILITY IN THE PRODUCTION OF BUNCHES.

The mean number of bunches of fruits produced per tree for the two years 1922–3 was 13·3, with a coefficient of variability of 52·9. *A priori* considerations suggest that two factors would exercise a predominant influence in determining the number of bunches of fruits, or what comes to the same thing, of female spadices. The first factor is the rate of leaf production, for this limits the possible rate of inflorescence production. Its importance can be assessed by calculating the correlation coefficient between the number of leaves produced in 1924 by different individuals, and their output of bunches of fruit for the two previous years. The value of the coefficient amounts to 0·45 ± ·055. A correlation of this degree might have been anticipated, and does not seem to call for comment.

Table II.

Frequency table for Sex-Ratios. Sex-Ratios expressed as percentage male spadices per 100 *spadices.*

Class value sex-ratio	Frequency	Class value sex-ratio	Frequency
5	1	55	9
15	–	65	6
25	1	75	14
35	1	85	18
45	3	95	24

The second factor is the *sex-ratio of the individual trees*, for this determines the proportion of the inflorescences that are female, and therefore the proportion that develop into bunches of fruits. For convenience in computing the correlation coefficients, the sex-ratios of the individual trees are expressed as the percentage of the total number of spadices that were male (Table II). Of the total number of flowering spadices produced by the whole population in 1924 approximately 76 per cent. were male, 22 per cent. were female, and 2 per cent. were bisexual. The latter type of spadix tends to be restricted to certain individuals. One individual, for instance, produced 21·4 per cent. of bisexual spadices. Bisexual inflorescences have been omitted in calculating the sex-ratios of individual trees. Eleven trees out of the whole population produced no female inflorescences in the course of the year, whereas every tree produced male spadices (Table II). The causes of this variability in the sex-ratio are obscure, but inasmuch as there is a small negative correlation (— 0·22 ± ·073) between the number of leaves

produced in 1924 and the sex-ratio for the same period, it would appear that the physiological level may play some part. The correlation coefficient suggests that individuals that produce a large number of leaves also tend to mature a relatively large proportion of female inflorescences.

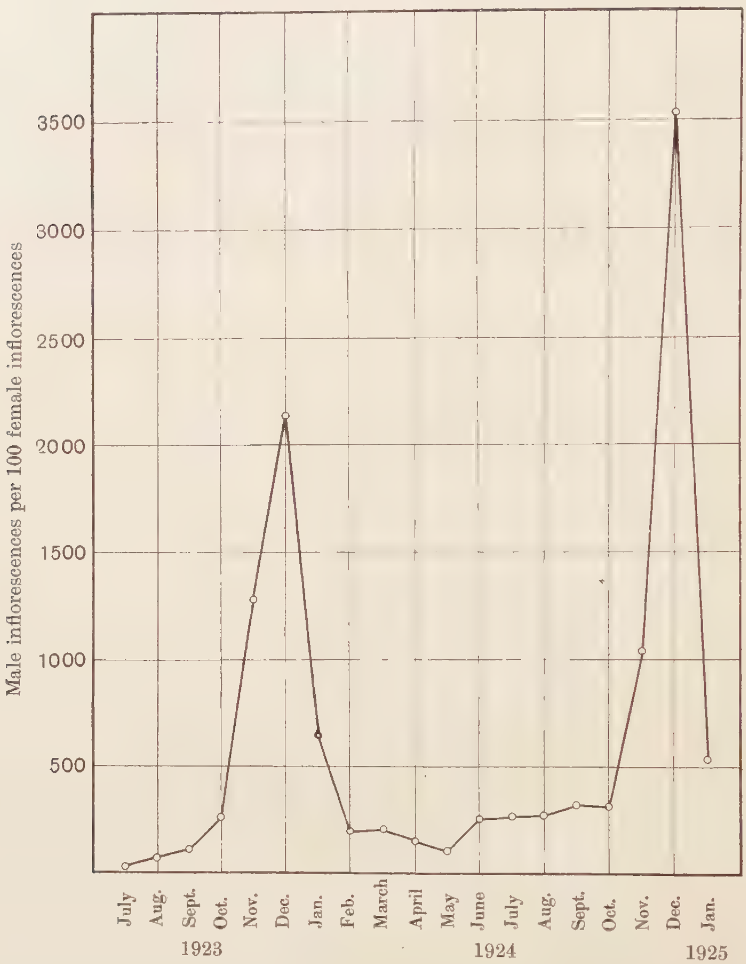

Fig. 3. Periodicity in sex-ratio for the whole population.

The main factors differentiating the sex of trees are, however, probably genetic. As the correlation between the sex-ratio for 1924 and the total number of bunches produced in the two previous years amounts to $-0{\cdot}40 \pm {\cdot}065$, it would appear that the sex-ratio of individuals does not fluctuate very markedly from one year to another, and that the

sex-ratio may be an important factor in determining the yield of bunches of fruits; trees with a high *proportion* of female inflorescences tend to produce a large number of bunches of fruits.

Seasonal Change in Sex-Ratio.

While the sex-ratio of individuals does not fluctuate markedly from year to year there is a distinct seasonal periodicity in the sex-ratio of the population. Fig. 3 illustrates the regular nature of this periodicity. Normally there is a considerable excess of male spadices; this is especially marked in December. Though there are doubtless seasonal changes in the differentiation of the sexes, it seems probable, that the great excess of male over female spadices in December is due to a tendency on the part of female inflorescences to abort before achieving anthesis. It is interesting to observe that the proportion of female inflorescences was greater in the autumn of 1923 than in 1924. There was a difference of over 11 inches of rainfall in the two years, 1924 being abnormally dry. It may be that this was the cause of the higher proportion of female inflorescences in the former year. It is possible, however, that the age factor may have some bearing in this connection.

Summary.

The work reported in this paper constitutes a first attempt to study the growth processes in a tropical palm. Three points of primary interest have come to light in the course of the investigation.

(1) In the first place it has been found that young trees have two flowering cycles in the course of the year, one in the autumn and the other in the spring. The modes of the flowering cycles correspond closely to the two periods of equal day and night. The correspondence is remarkable in view of the latitude of Ibadan, viz. 7° 22′ 30″. The suggestion was made that two distinct groups of environmental factors control the seasonal flowering cycles. The first group determines the laying down of the inflorescence primordia and is doubtless identical with that affecting leaf production. The annual distribution of rainfall is unquestionably the most important factor in this group. The second group of factors is active in promoting the actual flowering of the inflorescences. It is suggested that the relative length of day and night is a factor of paramount importance here.

(2) Secondly it has been ascertained that as trees age, there is a tendency for the spring flowering cycle to be eliminated. The suppression of the spring cycle seems to be correlated with an increase in the weight

of the individual bunches. This correlation only obtains until the trees are 30–40 feet in height, after which senescence is probably a factor in the economy of the palm. It is suggested that the increasing weight of the individual bunches leads to the exhaustion of food reserves. The strain of maturing the fruits that develop from the autumn flowering cycle must be considerable, for the growth of these fruits takes place in the dry season. It is considered that this exhaustion of the plant's reserves may be responsible for a shortage of female spadices during the spring period of equal day and night.

(3) The third point of interest is the sex-ratio. *The sex-ratios of the individual* trees were found to vary greatly. Some trees were completely male throughout 1924, but none were completely female. A few trees produce a large proportion of bisexual spadices. It was noticed that there was a slight tendency on the part of individuals that were especially active in the production of leaves to have a relatively high proportion of female spadices. It seems probable that though genetic factors are of chief importance in determining the differences observed in the sex-ratios, yet the influence of the individual's environment is by no means negligible. It would appear that the relative sex-ratios of the trees do not fluctuate very markedly from year to year, for the correlation coefficient between the sex-ratios of the trees in 1924 and number of bunches produced in the preceding two years amounts to $-0{\cdot}40 \pm {\cdot}065$. It is therefore concluded that the sex-ratio is an important factor in determining the yield of bunches of fruits; relatively female trees tend to produce a large number.

It has been found that the *sex-ratio of the population shows* a somewhat regular seasonal periodicity. Almost invariably there is an excess of male inflorescences, but this excess becomes particularly accentuated in December. Our data do not permit us to judge to what extent the December excess of males is due to a relatively greater mortality of young female spadices at this time, and to what extent it is due to a true periodicity in the differentiation of sex. It was observed that there was a larger proportion of female spadices in the autumn cycle of 1923 than in that of 1924. Again we are unable to decide to what extent this was due to differences in climate in the two years and to what extent to the age of the trees.

In conclusion we have pleasure in acknowledging our indebtedness to the Surveyor-General, Nigeria, for his courtesy in supplying us with particulars of the relative length of day and night at Ibadan.

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THE TRANSMISSION OF STREAK DISEASE OF MAIZE BY THE LEAFHOPPER *BALCLUTHA MBILA* NAUDE

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(With Plates XV–XVII.)

CONTENTS.

Introduction.

Within recent years there has been recognised a group of plant diseases, which, although transferable experimentally, have failed in microscopic or cultural study to give evidence of a recognisable parasite. In the denomination of this unknown pathogenic agent the term *virus* has acquired a special significance. The virus of certain of these diseases has been shown to pass a filter capable of holding back the smallest visible bacteria; the majority of workers now regard the virus as an organism which exists, at least during a part of its life-cycle, as particles of ultra-microscopic size.

Although known only by their effects, the plant virus diseases form a well-marked group, with many characters common to all. In general,

infection of a plant results in a derangement of its normal growth processes, without causing the death of any part. The most frequent visible effect is upon the chlorophyll-forming mechanism, producing partial chlorosis, noticeable as a mottled or mosaic pattern upon the leaves. In many cases reduction of power of growth may be extreme, so that stunted and malformed leaves develop, frequently massed to give a rosette-like form.

While certain of the virus diseases may be experimentally transmitted by mechanical juice transfer, the natural mode of spread appears to be by the agency of suctorial insects. In many cases infection by simple juice transfer can be obtained only with great difficulty or not at all. Transmission of some virus diseases is said to be restricted to insects belonging to a single species; especial interest attaches to these cases, since this obligate relationship between the disease and the insect-vector appears to indicate a necessity for the development of the virus within the insect. A close study of such cases may be expected to yield information concerning the nature of the virus, and the manner of its action within its insect and plant hosts.

A streak disease of sugar-cane, maize and related grasses, originally recorded in maize in 1901 by Fuller (2), was described by me in a recent paper (9), in which I advanced the opinion that it was a specific transmissible disease and to be associated with the virus diseases of the mosaic-type. This association was based upon the absence of a visible causative organism, and upon a general similarity in respect of the manner of spread and course of development to certain well-known diseases of the virus group, and in particular to the mosaic disease of maize, sugar-cane and other grasses. Confirmation of this view by experimental transmission of the disease under controlled conditions had not then been obtained; the present paper records experiments in which the transmission has been effected through the agency of a leaf-hopper of the family JASSIDAE.

This jassid, *Balclutha mbila* Naude, has been recently described for the first time from specimens which have been employed in this work[1].

[1] The following preliminary description has been published by T. J. Naude (*S. African Journal of Nat. Hist.* IV, No. 5 (1924), 307).

"*Balclutha mbila* sp.n.

"A small species with an average length of 3 mm. and an average width of 0·7 mm. across the widest part of the head; general colour dark brown with a conspicuous lighter medio-longitudinal band.

"Colour. Dorsal: Vertex lemon-yellow with two sub-circular black spots on the anterior margin; pronotum lemon-yellow medially, dark brown laterally; scutellum lemon-yellow;

In the following paper it will be shown that at certain seasons many of the leafhoppers of this species which may be collected on streak-diseased maize plants in the field are capable of producing the disease in every healthy plant upon which they subsequently feed; that hoppers of this species which have been reared from the egg solely upon healthy maize are incapable of infecting any maize plant, but may become infective after feeding upon a diseased plant. All trials of other suctorial insects, aphids, other jassids and fulgorids, have failed in every case to give infection of streak disease.

The vectors of the majority of virus diseases which have been studied have been found to be aphids. Transmission by jassids has been previously recorded only in a few instances; in particular the relation of *Eutettix tenella* Baker to sugar-beet curly-top disease has received full investigation by American workers (see, for example, Carsner and Stahl (1)); Kunkel (4) has reported transfer of aster yellows by *Cicadula sex-notata* Fall., and Murphy (5) of potato leaf-roll by *Typhlocyba ulmi.* The present work adds one more to this short list of jassid-borne virus diseases.

Consideration will be confined in this paper to the disease as it occurs in maize. Transmission between maize and other species of the Gramineae has been obtained only irregularly and is governed by conditions which are not yet understood.

The investigations upon which this paper is based were carried out at the Natal Herbarium, Durban, during the year 1924. While this work is entirely of my own initiation and development and I am therefore responsible for all the conclusions which have been drawn, I desire to acknowledge helpful criticism and much encouragement from the Chief of my Division, Dr I. B. Pole Evans. Thanks are also due to my assistants, Mr J. S. Mackay and Mr C. E. Levett, for help in field and experimental work.

The Development of the Disease.

Streak disease, when fully developed in the maize plant, is characterised by a pronounced chlorosis of the leaves confined to narrow broken stripes arranged along the veins (Fig. 1). The stripes vary from a few millimetres to several centimetres in length, and are individually from 0·5 to 1 mm. in width, although frequently fusing laterally to form wider

elytra dark brown with broad hyaline margins; abdomen black. Ventral: lemon-yellow to white, tip of ovipositor black.

"Vertex produced, angularly rounded anteriorly. Elytra exceeding abdomen by one-third of their length; appendix narrow."

composite stripes (Fig. 2). The chlorotic tissue generally appears an opaque yellow when viewed by transmitted light, affording a marked contrast to the deep green of the remainder of the leaf. On some leaves a small proportion of the stripes may appear translucent, and in this case the tissue may be slightly shrunken. The stripes are nearly evenly distributed over every leaf formed since the plant became diseased.

This disease appears not to be transmitted by the seed. This conclusion was reached by Fuller (2) in his original account of the disease and was confirmed by me (9). No case has been observed where the earliest leaves of a maize seedling were not quite free from the specific chlorotic markings of streak disease. Observations have shown the disease normally to take the following course. The first sign of the disease in an individual plant is the appearance of nearly colourless spots, generally almost circular, about 0·5 to 2 mm. in diameter, upon the lowest exposed portions of the youngest leaves (Fig. 3). These earliest spots are generally widely scattered, frequently separated by two or three centimetres. As more of each leaf becomes exposed by growth the youngest portions exhibit a progressive increase in the frequency of the spots, which now show a more or less elongation in the line of the leaf-veins. At this stage they may be evenly distributed over the basal portion of the leaf or confined to tracts following groups of leaf-veins (Fig. 4). Soon, however, the spotting becomes general over the whole of the base of the leaf, and continues to appear at uniform frequency over all the new leaves subsequently formed (Fig. 5). The chlorotic areas are delimited before the leaf unfolds, and no alteration in their size or shape occurs after the leaf has attained its full growth.

In conformity with this course of development, every diseased plant may be expected to bear some fully green leaves at its base. But the number of such fully green leaves varies greatly in different cases, and plants may be seen in the field in all stages, from that in which only the two lowermost leaves are entirely unaffected with streak markings, to that in which the only signs of the disease are a few insignificant colourless spots towards the base of the last leaf formed before the tassel appeared. (Compare Pls. XV, XVII, figs. 1 and 5.)

These observations are consistent with the view that streak is a disease, infection by which occurs at some stage subsequent to exposure of the aerial parts of the plant.

Experiments on the Exclusion of Insects from Growing Plants.

It was recorded in my paper (9) that maize plants raised in soil in tin containers, which were kept within an insect-proof greenhouse, remained unaffected with streak disease; but that they developed streak disease in a short time upon removal of the tins to the vicinity of a plot of diseased maize in the open. Experiments were carried out in this plot, in which maize plants were protected from the time of their appearance above ground by cylindrical cages of wire-gauze, closed at the upper end, and with the lower end sunk three inches into the soil. A complete internal lining of wire-netting of half-inch mesh, fixed at a distance of half an inch from the wire-gauze, prevented any foliage from coming into contact with the wire-gauze. Four sizes of gauze were used, two cages of each size, as follows:

6	holes to the inch—average size of each hole	·125	inch square.
16	,, ,, ,, ,, ,, ,, ,,	·052	,, ,,
30	,, ,, ,, ,, ,, ,, ,,	·026	,, ,,
52	,, ,, ,, ,, ,, ,, ,,	·013	,, ,,

Since the internal lining of wire-netting prevented any insect from reaching any part of the caged plants without passing bodily through the gauze, it was anticipated that the experiment would indicate the size of any insect or insects concerned in the transmission of the disease.

The first experiment was started on March 4th, 1924. By March 24th the first cases of disease began to appear in the exposed control plants, and, by the 31st, 75 per cent. were streaked. Meanwhile the disease had appeared in the cages of the largest mesh, and, by April 14th, in the cages of 16 meshes to the inch. The experiment was discontinued at the end of April, at which time all the plants in the cages of the two finer meshes were still healthy, while all the exposed controls were diseased.

This experiment was repeated upon maize planted on April 28th. Again all exposed control plants and those in the cages of the largest mesh became streaked within a month; the plants in the cages of the 16 meshes to the inch remained for a longer period healthy, but by August 1st they also were streaked. Within the two latter cages adults of *Balclutha mbila* were found, and a trial showed their ability to pass through gauze of 16 meshes to the inch. No other suctorial insects were present in these cages. Again the cages of 30 and 52 meshes contained healthy plants, and a careful search revealed no leafhoppers or other insects within them.

Experiments with *Balclutha mbila* Naude.

Cage Experiments.

Maize plants were raised from seed within muslin-covered cages, the sides of which were sunk two or three inches into the soil. From the time of their appearance above the ground until the conclusion of the experiment, the plants remained protected by the muslin, except during short periods of opening for inspection.

On April 4th, 1924, four adults of *Balclutha mbila*, collected upon diseased maize, were introduced into a cage containing three maize plants. All three plants had become fully streaked by April 25th. This experiment was repeated five times within the next month. In four of the cages used in these experiments the first signs of streak disease appeared in about 14 days, and all the plants subsequently became diseased. In one cage the plants remained healthy for three months. The reason for the failure of the latter is not known, but it should be recorded that after the first introduction, no hoppers were seen feeding upon the maize, whereas in the other cages individuals were to be seen at every examination.

Meanwhile the plants in three cages, to which no hoppers were introduced, remained healthy for three months. A further control experiment was carried out with three adult *Balclutha mbila*, which were collected upon a healthy maize plant growing in the greenhouse. The origin of the hoppers was unknown, but, since no streak-diseased maize had been present in the house, it was reasonable to suppose that they had not fed upon diseased maize. These hoppers were placed upon plants protected by a cage and the plants remained healthy for two months, although the hoppers were seen feeding frequently during this period.

Greenhouse Experiments.

(*a*) *Experimental Method.* The preliminary cage experiments were followed by investigations employing a more exact technique, in which I studied the effect of allowing an individual hopper to feed upon a portion of one leaf of the experimental plant. Single hoppers were placed in glass tubes, about 8 inches long by 1 inch diameter, closed at one end by fine muslin and at the other by a plug of cotton wool, through which passed the leaf of the experimental plant (Pl. XVII, fig. 6). The introduction of the leaf could be effected with safety while the hopper was resting at the top of the tube. At the end of the experiment the portion of the leaf exposed was cut off from the main plant below the wool plug, and

either the tube and its contents were removed from the greenhouse or the piece of leaf was plunged into disinfectant. All the experiments in this series were carried out upon plants raised from seed in tins of soil in a greenhouse which had been fumigated and rendered as nearly insect-proof as possible by means of wire-gauze over the windows. In spite of the precautions taken, aphids gained entrance in some manner unknown and one or two minor outbreaks occurred of *Macrosiphum granarium* Kirby and *Aphis sacchari* Zehntner, which were dealt with at once by destruction of the affected plants or by spraying. Four hoppers escaped while experiments were in progress, but all four were recaptured within a day or two upon plants adjacent to the spot where the escape took place. One however during the period of freedom carried the disease to a control plant. Apart from these four, no hoppers were found at large in the greenhouse during the period of the experiments.

The shading necessary to prevent undue condensation of moisture upon the walls of the tubes, combined with the somewhat deficient ventilation of the house consequent upon the need for insect-proofing, caused the plants to be rather tender and drawn. They were, however, of a good colour and by no means sickly.

(*b*) *Results with Adults collected upon Diseased Maize.* The hoppers used were adults collected during the months April to August, 1924, in maize plots, wherein practically all of the plants were streak-diseased. While nothing definite was known of the history of these insects, it is almost inevitable that all had fed at some time upon diseased maize, and likely that their whole development had been passed on diseased plants.

The results of this series of experiments may be summarised as follows. The feeding individually of twelve adults (2 males and 10 females) for periods of five hours or more (generally about a week), each upon the tip of a single leaf of the experimental plant, caused streak disease to appear in the young unfolding leaves of 46 plants, within a period of 7–26 days from the original exposure. No one of these twelve individuals failed to produce the disease in any plant to which it was transferred, except in two cases which are discussed later in this section. Meanwhile 58 out of 59 plants which were not subjected to the feeding of any hoppers remained healthy, although growing alongside, generally in the same tins as those experimentally infected in the manner described above. The one exception is that referred to earlier, being the identical plant upon which one of the escaped hoppers was recaptured.

Four examples of the records of individual hoppers, considerably condensed, are now given. Examples (*a*) and (*b*) are typical of the majority of the experiments which have been summarised above. In certain cases, however, the treatment was varied in different ways; example (*c*) shows the effect of starvation, (*d*) that of periodically feeding upon an apparently immune plant.

Maize of the variety Hickory King was employed throughout the series of experiments.

Example (*a*). *Balclutha mbila*, No. 28. ♂.

17. vi. 24.	Collected on streak-diseased maize, Durban. Placed on maize plant 18 days old. Plant became streaked in 26 days.
9. vii. 24.	Transferred to maize plant 26 days old. Plant became streaked in 21 days.
16. vii. 24.	Transferred to maize plant 33 days old. Plant became streaked in 22 days.
8. viii. 24.	Hopper dead.

Example (*b*). *Balclutha mbila*, No. 10. ♀.

28. iv. 24.	Collected on streak-diseased maize at Pinetown, Natal. Produced disease (with three other individuals) in cage experiments.
23. v. 24.	Placed on maize plant 16 days old. Plant became streaked in 14 days.
6. vi. 24.	Transferred to maize plant 16 days old. Plant became streaked in 17 days.
17. vi. 24.	Transferred to maize plant 18 days old. Plant became streaked in 29 days.
9. vii. 24.	Transferred to maize plant 25 days old. Plant became streaked in 17 days.
15. vii. 24.	Transferred to maize plant 26 days old. Plant became streaked in 15 days.
28. vii. 24.	Transferred to maize plant 90 days old. Plant tasselling in 10 days, without showing any marks of streak disease.
11. viii. 24.	Transferred to maize plant 10 days old. Plant became streaked in 14 days.
1. ix. 24.	Transferred to maize plant 24 days old. Plant remained healthy for 48 days.
13. ix. 24.	Transferred to maize plant 36 days old. Plant became streaked in 24 days.
26. ix. 24.	Hopper dead.

Example (*c*). *Balclutha mbila*, No. 30. ♀.

30. v. 24.	Collected on streak diseased maize, Durban. Produced disease (with three others) in cage experiments.
18. vi. 24.	Placed on maize plant 19 days old. Plant became streaked in 13 days.
2. vii. 24.	After starving for 20 hours, placed on maize plant 18 days old for 5 hours. Plant became streaked in 8 days.

3. vii. 24.	After starving for 18 hours, placed on maize plant 19 days old, for 8 hours. Plant became streaked in 7 days.
4. vii. 24.	After starving for 16 hours, placed on maize plant 20 days old, for 23 hours. Plant became streaked in 10 days.
5. vii. 24.	After starving for 1 hour, placed on maize plant 21 days old for 53 hours. Plant became streaked in 9 days.
7. vii. 24.	Transferred to maize plant 60 days old. Plant became streaked in 23 days.
14. vii. 24.	Hopper dead.

EXAMPLE (*d*). *Balclutha mbila*, No. 30. ♀.

17. vi. 24.	Collected on streak-diseased maize, Durban. Placed on maize plant 18 days old. Plant became streaked in 13 days.
1. vii. 24.	Transferred to sugar-cane (variety P.O.J. 36).
7. vii. 24.	Transferred to maize plant 23 days old. Plant became streaked in 12 days.
10. vii. 24.	Transferred back to sugar-cane.
17. vii. 24.	Transferred to maize plant 33 days old. Plant became streaked in 9 days.
19. vii. 24.	Transferred back to sugar-cane.
28. vii. 24.	Transferred to maize plant 44 days old. Plant became streaked in 8 days.
6. viii. 24.	Transferred back to sugar-cane.
16. viii. 24.	Transferred to maize plant 8 days old. Plant became streaked in 9 days.
21. viii. 24.	Transferred back to sugar-cane.
28. viii. 24.	Hopper dead.

Temperature of greenhouse during period of experiments:

Mean daily maximum	26° C.
Mean daily minimum	14° C.
Mean for whole period	20° C.

In these trials every individual of *Balclutha mbila*, once proved to be capable of infecting maize, did not fail to infect every plant upon which it was allowed to feed, except in two cases occurring in example (*b*). Of these failures however one is of no significance, being explicable by the cessation of growth consequent upon the development of the tassel before the symptoms would normally have had time to appear. The explanation is not clear of the failure, in example (*b*), of the hopper to produce the disease in the plant to which it was transferred on 1. ix. 24. The hopper undoubtedly fed upon this plant for twelve days, and was able subsequently to infect another plant.

Not all however of the hoppers collected upon fully-streaked maize were found to be infective. Three individuals, which were actually feeding upon diseased plants at the time of capture, proved to be incapable of producing the disease, although tested upon healthy maize plants, one five times, one three times and the third once. In the case of the first of these hoppers the period of testing extended over 127 days.

(*c*) *Results with Adults Reared upon Healthy Maize.* The work already described showed that the majority of the hoppers collected upon streak-diseased maize were capable of producing the disease in all healthy plants upon which they fed. Although the single cage experiment with hoppers taken from healthy plants gave no positive infections, yet it remained to be proved definitely that the power of producing the disease is not inherent in *Balclutha mbila*, but is acquired only as a result of feeding upon a diseased plant.

A supply of hoppers for the following experiments was obtained in three ways: (1) Certain non-infective individuals, referred to in the two previous sections, were allowed to lay eggs on healthy maize or cane plants and the progeny reared. (2) Proved infective individuals were allowed to lay eggs upon a sugar-cane plant. The plant remained healthy and the progeny was reared upon it. (3) The young, hatching from eggs laid by an infective female in the tissue of a leaf of a plant which subsequently developed streak, were removed within a day or two to a healthy plant. By this method there was a danger that the young individuals might have acquired infection from the old leaf before their removal from it. In order to escape this risk in their studies of the transmission of curly-top of sugar-beet by *Eutettix tenella* Baker, Stahl and Carsner (8) adopted a tedious technique of lifting the young hatching hoppers off the plant before their appendages had fully unfolded, and therefore before they had had an opportunity to feed. In the present work, the cruder method employed proved apparently to be effective, for the healthy maize plants to which the hoppers were transferred failed in every case to develop streak disease. Once a stock of non-infective hoppers had been established, no difficulty was experienced in breeding further supplies from eggs laid upon healthy maize by certain of these non-infective individuals.

Tests of adult hoppers reared on healthy maize were carried out, employing the technique described in the previous section. These experiments form an exact parallel to those done with the infective hoppers, and the environmental conditions were therefore not unfavourable to the development of the disease. Nineteen hoppers (8 males and 11 females) were allowed to feed for periods exceeding two days, and in some cases as long as 40 days, upon single leaves of 28 healthy maize plants, without producing streak disease in any plants during a period of observation varying between six weeks and two months.

Hoppers therefore which had fed only upon healthy maize or cane plants were incapable of infecting a plant with streak disease. Experi-

ments were next carried out with the purpose of showing that the power of producing streak disease was acquired by these hoppers after feeding upon diseased plants. Non-infective adults, bred from eggs by the methods already described, were placed in glass tubes and a fully-streaked maize leaf of a plant experimentally infected introduced through the cotton-wool plug. After feeding for approximately a week the hoppers were removed, separated singly into tubes, and each allowed to feed upon a leaf of a healthy maize plant for a period of about seven days. This work was carried out in the insect-proof greenhouse and the usual precautions as regards control plants were taken. The infective power of each hopper was judged by the appearance in the experimental plants of streak symptoms or their absence after a month's observation.

Table I.

Tests of Balclutha mbila *Naude, bred on healthy plants and allowed to feed for a limited period upon streak-diseased plants.*

Temperature of greenhouse: Mean daily maximum 29° C.
Mean daily minimum 20° C.
Mean for period 24·5° C.

Series No.	Origin of hoppers	No. of days on streaked leaf	No. of hoppers tested		No. of hoppers proved infective	
			Males	Females	Males	Females
I	1st and 2nd generation from infective female, reared on healthy maize	5–7	6	14	nil	13
II	1st generation from non-infective female, reared on healthy maize	8–9	8	8	nil	8
III	1st generation from non-infective female, reared on healthy maize	6	1	4	nil	nil
IV	1st generation from non-infective female, reared on healthy sugar-cane	10	8	—	3	—
V	1st generation from infective female, reared on healthy maize	7–15	4	9	4	9
			Percentage infective		26	86

The results of this work are presented in Table I. Of 62 hoppers tested, 37 acquired the power of infection after feeding upon the leaf of a diseased plant. Although both sexes became infective, the males did so in much lower proportion than the females. During the period upon the streak-diseased leaf, all the hoppers were to be seen resting on the leaf and apparently feeding; indeed it is improbable that they could

have survived for a week without feeding. In spite of this, however, nearly one half of the hoppers failed to become infective.

EXPERIMENTS WITH OTHER INSECTS.

The attempts to secure transfer of streak disease by the agency of various insects other than *Balclutha mbila* were unsuccessful. It was recorded earlier that the only suctorial insects which were to be found colonising streak-diseased maize in large numbers were *Aphis maidis* Fitch and *Peregrinus maidis* Ashmead. Both were to be regarded with suspicion, since *Aphis maidis* had been proved by several workers to be the vector of grass mosaic, and a similar claim had been made for *Peregrinus maidis* (3). At different times various fulgorids and jassids were collected on streak-diseased maize and were tested for transmission of the disease.

For the elimination of the insects incapable of transmitting the disease a simplified technique was mainly employed. A large number of the insects under investigation, obtained from diseased plants in the open, was introduced into a chamber of the greenhouse, and distributed over healthy plants therein. The insects were seen during subsequent days to be feeding upon the experimental plants, which were kept under observation within the greenhouse for a period of several months. The value of an experiment of this crude nature was mainly for the negative evidence which it afforded; any positive results would have done no more than indicate the direction in which further work might be prosecuted. The negative evidence, however, is considered to be trustworthy. The method allowed of the use of large numbers of the insects and the exposure of a reasonable number of plants to their feeding. Conditions were not unsuitable for the development of streak disease, since the successful *Balclutha* experiments were performed in an adjacent chamber of the greenhouse. Under similar conditions the transfer of sugar-cane mosaic was effected successfully by the agency of mosaic-infective *Aphis maidis*.

Aphis maidis Fitch. A trial of this aphid as a carrier of streak was made on two occasions by the greenhouse method. In each case several hundred aphids were introduced into the house with pieces of the streaked maize plant which they had colonised in the field. The aphids were of all ages, and winged and wingless adults were present. In the first trial all of 32 maize plants were healthy four months after the introduction. In the second experiment 48 plants, varying in age between

one and six weeks at the time of exposure, had developed no streak disease at the end of two months.

Subsequently this insect was tested by the muslin cage method, already described in reference to the *Balclutha* experiments. Aphids from streak-diseased maize were placed in two such cages, each containing three maize plants. All plants were healthy when discarded after two and three months respectively.

Peregrinus maidis Ashmead. This fulgorid was investigated in a similar manner. In a greenhouse experiment, no streak disease had appeared in 28 maize plants two months after the introduction. Two muslin cage trials gave similarly negative results after six weeks and two months.

Other Jassids and Fulgorids. About 60 adult jassids and fulgorids, collected on streak-diseased maize or sugar-cane, were tested upon healthy maize by the glass tube method, without producing the disease in any plants. Determinations of the insects have not yet been made, but probably more than 20 species were represented among the 60 individuals tested.

Field observations of *Balclutha mbila* Naude.

An hypothesis of the agency of any insect in the dissemination of a plant disease must be founded upon two facts; the transmission of the disease by the insect under experimental conditions, and the observation of the occurrence of the insect in the field at such time and place as to account for outbreaks of the disease. A selection of the results of searching for *Balclutha mbila* in a variety of localities is given in Table II. Whenever a thorough search has been made of streak-diseased maize in a young stage and under favourable weather conditions, specimens of this hopper have been collected.

This insect has therefore been found on all occasions in association with streak-disease outbreaks. Although probably the most abundant jassid upon the maize of the Natal coastal area, it has never been observed in large numbers. The adults are to be seen normally during daylight resting upon the upper surface of the young maize leaves forming the terminal cone of the plant. Although careful search has been made, adults have very rarely been found upon any other part of the maize plant. However the number of hoppers to be seen varies at different times of the day, so that they must have some resting place at present undiscovered, and it is uncertain how far the number of hoppers to be seen at any time represents the total hopper population of the field.

Table II.

Records of the occurrence of Balclutha mbila *Naude upon maize in different localities.*

Date	District	Locality	Elevation above sea-level ft.	State of maize crop	Occurrence of *Balclutha mbila*
March, 1924, to Feb., 1925	Natal coast	Durban	under 100	Succession of crops, which became diseased in a proportion of plants	Always a few present
Oct., Nov., 1924, and Jan., 1925	Natal coast	Umgeni	under 100	About 30 % diseased	Present
May, 1924	Natal coast	Umbogintwini	200	Entirely diseased	Present
Oct. to Jan., 1925	Natal coast	Umbogintwini	200	About 10 % diseased	Present
March to May, 1924	Natal midlands	Pinetown	1200	Entirely diseased	Present
May, 1924	Natal midlands	Richmond	2800	About 20 % diseased	Present
Oct., 1924	Zululand	Eshowe	1600	About 10 % diseased	Present
Jan., 1925	Northern Transvaal	Potgietersrust	3800	About 75 % diseased	Present

Estimates of the frequency of occurrence of *Balclutha mbila* are therefore subject to this uncertainty. In a series of observations carried out at intervals through the day in a plot of maize, where experience of sweeping with a net had shown the hoppers to be unusually abundant, the greatest number of adults seen averaged one hopper to eight maize plants. In general in the field an apparent frequency of one hopper to 20 plants is rarely exceeded.

Discussion.

From the foregoing results it is concluded that *Balclutha mbila* is capable of withdrawing a virus from a plant affected with streak disease, of retaining that virus for a long period, and of injecting it into other plants upon which it subsequently feeds. In all probability no other common Natal maize-feeding insect is capable of effecting the transfer of the virus. A specific relationship appears to exist therefore between the virus of streak and this particular insect, analogous to that found in certain of the other virus diseases.

The virus, injected by the hopper, presumably passed down the leaf and eventually reached the growing point; its effect was never to be seen upon the old leaf into which it was injected, but only in the young

leaves formed since the infection occurred. This course of development, typical generally of the virus diseases, was strikingly brought out by the particular experimental technique employed.

The cage method of experiment, used generally by workers in this field, is open to several objections: the difficulty of manipulating so agile an insect as a jassid in a large cage; the need for leaving the plant caged for the whole incubation period, and consequent large expense incurred in providing a sufficient number of cages; the complication which may result if reproduction takes place within the cages; the inability of the experimenter to determine upon what part of the plant the insect has fed.

In the present investigation the cage method was rejected after the preliminary trials in favour of the glass-tube technique. The reliability of the results of this technique depends upon the insect-free condition of the greenhouse in which incubation of the disease took place in the plants, which were not otherwise protected. The main sources of danger were from insects gaining entry into the house and from the accidental escape of experimental insects. The exclusion of insects from outside was unfortunately not fully achieved, although an approximation to it was obtained. The escapes occurred while the technique was in the trial stage, and were occasioned by the accidental withdrawal of the wool plug or the perishing of the rubber band holding the muslin in place. No escapes occurred during manipulation, the hopper being readily induced to move to the top of the comparatively long tube, when the wool plug could be withdrawn without risk. The safe manipulation of hoppers in the shallow glass vessel used by Severin (7) would appear to be difficult. The precaution of destroying at the end of the experiment the portion of the leaf which had been exposed to the feeding of the hoppers ensured the destruction of any eggs which might have been laid in the leaf-tissue or any young which might have hatched. Severin (*loc. cit.*) used only male hoppers in order to avoid complications from egg-laying, but my method allowed of the use of either sex indifferently. In experiments involving only a very short exposure to the feeding of the hoppers, the cutting off of the leaf might have introduced a complicating factor, but in this investigation ample time was allowed, and there is no evidence to suggest that the results were influenced by this procedure.

A full number of control plants was grown under conditions exactly similar to those of the experimental plants upon which the hoppers were allowed to feed, and all remained healthy with the exception of

one plant, upon which was found an escaped infective hopper. The appearance of the disease in the experimental plants cannot therefore be attributed to any cause other than the feeding of the leafhoppers.

In one respect streak is an exceptionally favourable disease for experimental study. The symptoms are of so pronounced a character that there cannot be any doubt whether infection of a plant has occurred. The variability of the symptoms of the virus diseases of the potato plant under different conditions has added greatly to the difficulty of the study of these diseases; in the mosaic of sugar-cane and maize the symptoms may be so faint as to render diagnosis uncertain. But under all the conditions which have been encountered, the symptoms of streak have been so clear as to allow of no doubt in their recognition.

The regularity with which single individuals of *Balclutha mbila* caused infection is in marked contrast to the experience generally in virus disease transmission. Severin (7), for example, found that individuals of *Eutettix tenella*, transferred to new healthy beet seedlings daily, might fail to infect any plants for periods up to 21 days. On the other hand, the ability of a single hopper to produce the disease in its severest form is not surprising, Carsner and Stahl (1) finding no difference in the severity of the curly-top infection resulting from the feeding of one infective beet leafhopper or of ten leafhoppers.

The occurrence has been shown of individuals of *Balclutha mbila*, which failed under apparently favourable conditions to become infective. The details in the second column of Table I remove the possibility of an explanation of this observation upon grounds of an incorrect determination of a species close to *Balclutha mbila*, for the progeny of infective parents included individuals which resisted infection. Whatever be the explanation of these refractory individuals, the realisation of their existence is of great importance in experimental work.

It might be held that the relative infrequency of the occurrence of *Balclutha mbila* in the field discounted its importance in the dissemination of streak disease. This objection is not supported, however, by the experience with the jassid-transmitted curly-top disease, Schwing and Hartung (6) regarding an infestation of one *Eutettix tenella* to 20 beet plants at the time of thinning to be sufficient to ensure a failure of the crop. Furthermore, *Balclutha mbila* has given evidence of being a highly efficient vector of disease. Under experimental conditions one individual lived for five months and did not lose the power of disease-transmission during that period. The disease was produced by the feeding of an infective hopper for five hours, and under suitable circumstances it is

likely that a shorter period would suffice. In view of these facts and the great agility of the adult hopper, the potentiality for disease-dissemination of the individual is considered to be high, and a comparatively small number of infective hoppers is likely to be able to carry infection throughout a plot of maize.

Summary.

In the absence of transmission of streak disease by the seed, the wide occurrence of this disease in maize in South Africa is accounted for by infection of the plants at some period after their appearance above ground. It has been shown that plants may be protected from infection by growing them in a greenhouse or under wire-gauze of not less than 32 meshes to the inch.

A number of insects have been tested as possible vectors of streak disease, and positive results have been obtained with a jassid, *Balclutha mbila* Naude. In four cages out of five, to each of which were introduced three or four adults of this species, collected on streak-diseased maize, the disease developed in every plant. The plants in three similar cages, to which no jassids were introduced, remained healthy.

In experiments in which single individuals of *Balclutha mbila*, collected upon streak-diseased maize, were allowed to feed upon single leaves of the experimental plants, the disease resulted in 46 out of 48 plants. One jassid lived for five months and carried the disease to eight separate plants. No loss of the power of infection occurred in any jassid tested, in spite of periods of starvation in some cases or of feeding on apparently immune plants in others. Certain individuals, collected upon streaked maize were incapable of causing any infection under similar conditions.

Jassids reared upon healthy maize were incapable of infecting plants with streak disease. But after feeding upon a diseased leaf for a week, 26 per cent. of the males and 86 per cent of the females, out of a total of 62 individuals, became infective.

Negative results were obtained in trials of *Aphis maidis* Fitch, *Peregrinus maidis* Ashmead and a number of undetermined jassids and fulgorids.

Field observations showed that *Balclutha mbila* was to be found, although infrequently, whenever a field of maize, recently infected with streak disease, was thoroughly searched. It is held therefore to be the agent of spread of the disease in the field.

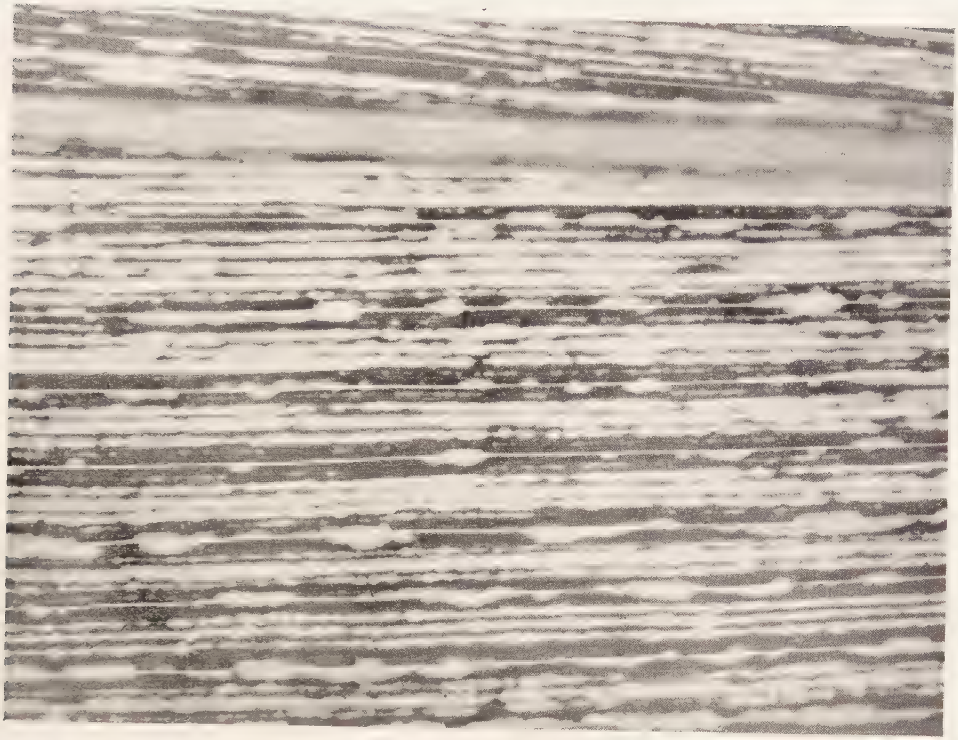

Fig. 2.

Fig. 1.

STOREY.—The Transmission of Streak Disease of Maize by the Leafhopper. (pp. 422–439.)

Fig. 4.

Fig. 3.

STOREY.—THE TRANSMISSION OF STREAK DISEASE OF MAIZE BY THE LEAFHOPPER. (pp. 422–439.)

Fig. 5.

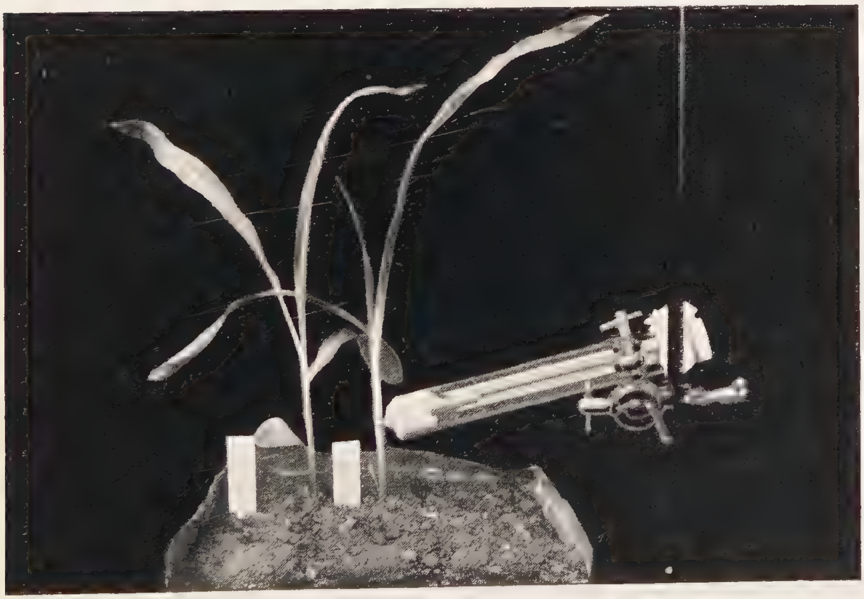

Fig. 6.

STOREY.—THE TRANSMISSION OF STREAK DISEASE OF MAIZE BY THE LEAFHOPPER. (pp. 422–439.)

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EXPLANATION OF PLATES XV—XVII

Fig. 1. Streak disease fully developed. A maize plant naturally infected in the open at an early stage of growth, showing the typical disease pattern. (One-fifth natural size.)

Fig. 2. The streak disease pattern. Portion of a streaked maize leaf, photographed by transmitted light, showing chlorotic stripes following the leaf-veins and frequently fusing laterally. (Four times natural size.)

Fig. 3. The first signs of streak disease. A maize seedling, experimentally infected, with scattered, nearly circular, colourless spots on the young leaves. Towards the base of the youngest leaf the typical streak pattern is beginning to appear. (One-half natural size.)

Fig. 4. The development of streak disease. A maize plant, naturally infected in the open, in a more advanced stage of development of streak than Fig. 3. The streak pattern is confined to tracts of the leaf surface. (One-fourth natural size.)

Fig. 5. The development of streak disease. A more advanced stage than Fig. 4. The whole of the youngest leaf is fully streaked. (One-sixth natural size.)

Fig. 6. The experimental method of streak disease transmission. The glass tube contains an infective *Balclutha mbila*, which has fed upon the introduced leaf-tip for ten days. Note the streak symptoms appearing in the young leaves of this plant, and the healthiness of the control plant growing in the same tin. The plants are somewhat drawn owing to the artificial conditions of the insect-proof greenhouse. (One-fourth natural size.)

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PHYSIOLOGICAL PRE-DETERMINATION EXPERIMENTS WITH CERTAIN ECONOMIC CROPS[1]

THE RELATION BETWEEN RATE OF GERMINATION AND SUBSEQUENT GROWTH

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(With Plate XVIII and 1 Text-figure.)

CONTENTS.

Introduction.

The economic importance attached to the almost universal practice of seed-testing has directed the attention of many workers to problems of the seed, its maturation and germination under varied conditions. A considerable literature exists dealing both with the technique of seed-testing under normal conditions, and with the germination of the seed under all manner of artificial conditions. It would seem, however, that comparatively few have traced the development of the seedlings produced from tested seeds beyond the very earliest stages.

[1] Part of this paper constituted a thesis for the M.Sc. degree, London, 1924.

A comprehensive review and analysis of the literature dealing with the influence of physiological conditions of the seed upon the subsequent growth and yield of the plants produced, has been made by Kidd and West (14)[1]. Summarising their chapter upon the effect of soaking seeds in water, they state that soaking has a marked effect upon the subsequent growth of the plant, and that "a germination test cannot be relied upon in the least to give any criterion of what this effect may be." They further point out that the nature of the effect is specific and cite the contrasting effects of soaking upon *Vicia faba* and *Phaseolus vulgaris* as an example.

Precise information as to the total number of viable seeds is readily obtained in a germination test under laboratory conditions. The value of seed-testing would be greatly increased if reliable information as to the potential growth of seed under normal conditions could be gauged by a simple laboratory test.

Davidson and Stapledon (6) investigating the failure of Black Yeo Oats in Glamorgan in 1921 found that the seed when tested gave high total germination figures. The rate of germination was slow. The seedlings produced in the fields were not vigorous enough to persist under the unfavourable moisture conditions prevailing in the locality during that season. They suggest that additional protection would be provided if information as to the energy of tested samples was also given to the practical grower by the Seed Testing Stations. For such information to be of value a definite relationship between "energy of germination"[2] and subsequent growth must be shown to exist.

The experiments to be described form an attempt to discover under varying conditions how far this relationship does exist in the case of a few economic crops. The problem was approached by a consideration of some of the factors that influence the rate of germination, and attempts were made to trace the influence of such factors upon growth. Special attention was given to soaking as an aid to early germination. The seeds were Cereals (particularly Oats), Grasses and some economic Leguminoseae.

[1] Reference by number to literature cited.

[2] The term "energy of germination" is employed by the writer to mean an index of rapidity of germination. The selection of any particular index for general use can only take place after the relationship between rate of germination and subsequent growth has been studied.

I. The Effect of the State of Maturity of the Seed, Husk Removal, and Drying, upon the Germination of Oats.

Samples of Grey Winter Oats were harvested from different areas of the same plot (to get a thoroughly representative sample) at three stages of ripening and their germination tested immediately after harvesting. The results are shown in Table I, for both complete grain and grain that was shelled by hand carefully.

Table I.

Effect of State of Ripeness and Husk removal upon Germination.

				% germination					
				Complete grain			Husk removed. Naked caryopses		
Date and sample index	State of "ripeness"	% moisture in grain	No. tested	3rd day	5th day	Total	3rd day	5th day	Total
4. viii. 23. A	50 % glumes green. Only upper spikelets ripe	26·4	1000. 10 tests of 100	0	12	23	4	23	43
18. viii. 23. B	No green glumes—all ripe—all straw quite yellow	22·4	,,	1	13	57	14	46	67
1. ix. 23. C	Plot cut 23. viii. 23, in stook from 24. viii. 23, taken from stook	25·7	,,	1	69	90	1	65	87

During the fortnightly intervals between harvesting exceptionally wet weather occurred so that little drying was possible, and no steady decline in the moisture content took place. Harlan and Pope (10) have traced out the relation of water content to maturity in barley, and in several varieties they obtained a steady decline from the time of flowering to maturity in the percentage of water present in the grain. In the above experiment, however, maturation, in so far as it is expressed by germination, has proceeded despite fluctuations in the moisture content, there being no steady decline. A steady decline in moisture content is not considered to be necessary for, nor the cause of, maturation. Whilst Table I shows that husk removal gives a marked increase in both energy and total figures, husk removal from a very immature sample does not make its germination approach that of a more mature sample.

Difficulty in obtaining satisfactory germination tests with freshly-harvested grain required for immediate autumn sowing, has led to the adoption of various means to force the germination. Each of the above samples, A, B and C, was subjected to the following treatments:

(1) Heating for five days at 40° C. in the dry atmosphere of an incubator.

(2) Desiccation over pure sulphuric acid at 22° C. to 8 per cent. moisture (approximately).

(3) An attempt was made to reduce the water content to a uniform percentage—5 per cent.—by heating at 40° C.

After treatment germination tests of both complete and shelled[1] grain were carried out.

The following is a summary of these germination tests in which five separate samples of 100 were used in each case:

Table II.

The Effect of Drying on the Germination of Mature and Immature Grain—Grey Winter Oats.

Sample and treatment	Treatment and duration	% H_2O left	% germination: Complete grain 3rd day	5th day	Total	Caryopses only 3rd day	5th day	Total
4. viii. 23. Control A		26·41	0	12	23	4	23	43
A 1	Heated at 40° C. for 5 days	2·66	11	76	80	22	78	86
A 2	10 days' desiccation	6·90	0	40	93	5	32	88
A 3	40° C. 1½ days	4·18	10	21	48	18	33	67
18. viii. 23. Control B		22·4	1	13	57	14	46	67
B 1	Heated at 40° C. for 5 days	4·03	0	34	100	0	19	92
B 2	7 days' desiccation	8·09	1	66	95	4	75	96
B 3	40° C. 1 day	5·10	1	58	85	0	35	65
1. ix. 23. Control C		25·7	1	69	90	1	65	87
C 1	Heated at 40° C. for 5 days	3·7	0	63	93	0	74	93
C 2	11 days' desiccation	9·3	1	81	93	4	86	94
C 3	40° C. 1 day	6·3	0	68	91	2	61	88

Confirmatory tests were obtained by another series of experiments with Radnorshire Sprig Oats.

From Table II it is seen that a marked increase in both energy and total germination is produced by all the methods of drying employed—especially in the most immature sample (A), where the total germination percentage has jumped from 23–80 per cent. after drying for 5 days.

[1] Husk removal after treatment prior to germination test.

Reduction of the moisture content to approximately the same percentage does not produce equal germination figures in the different samples so that after-ripening does not consist in mere water removal. Even heating for such short periods as $1\frac{1}{2}$ days (A 3) and 1 day (B 3) has produced a marked improvement upon the early harvested samples, an increase of 25 per cent. being noted in the total figure (compare A and A 3). Although heating for five days at 40° C. produces a more marked effect than does desiccation on the fifth day figures of the youngest sample (A), yet the total germination is better with the slow treatment even in this case, prolonged exposure to the higher temperature kills the weaker grain no doubt. The total figures of the more mature samples also do not point to a marked advantage of heating over desiccation. Husk removal (prior to germination) has facilitated germination and tended to mask the effect of the drying treatments.

The beneficial effects of drying as an aid to germination have been pointed out by other workers. Stapledon and Adams (19) obtained increased germination by heating good grain. Hiltner (11) has shown that drying without heating—he employed sulphuric acid as a desiccator—hastens after-ripening. Harrington (8) more recently has obtained increased germination of cereals by similar methods. Greig (7) noted the beneficial effect of drying in the fields upon germination and compared oats harvested in wet weather in Aberdeen with those harvested in dry conditions in Cambridgeshire. Brown (4) has demonstrated the existence of a semi-permeable membrane in the coat covering of the oat as well as in other Gramineae. Genetical work with wheat by Nilsson-Ehle (17) has shown that slow after-ripening of wheat is correlated with the presence of red colour in the caryopsis coat, and that this delayed germination character (or "germination resistance") is a Mendelian segregating character. White and "one factored" red varieties of grain showed somewhat more rapid absorption of water than the "many factored" red varieties. In the absence of the "red factor" the coat appeared to have a more delicate character so that the red colouring matter in itself does not appear to be the only cause of delayed germination. Atwood (1), working with Wild Oats, *A. Fatua*, has demonstrated that the limiting factor causing delayed germination is a poor oxygen supply. Crocker (5) emphasised the importance of the rôle of the seed coat and states that seed coats which exclude water are much better adapted to secure delayed germination than even those which exclude oxygen. Recent work on Johnson grass by Crocker and Harrington (9) confirms the importance of the resistance of the

caryopsis coverings to water imbibition as a factor causing delayed germination.

That some permanent change has been brought about by the treatments was shown by allowing the control and treated samples to stand exposed to laboratory conditions for a period of seven weeks; the treated samples gradually took up water until their moisture content approached that of the controls again. On now testing their germination it was still found that the treated samples gave higher "energy" and total figures than the controls which had of course vastly improved. It is again seen that after-ripening as measured by germination is independent of the water content. Table III is a summary of these germination tests performed after re-absorption of water by the seed which was previously treated:

Table III.

Germination Tests after Re-absorption of Water by Treated Samples. Controls now more "mature."

			Complete grain			Husk off		
Date	Sample	% moisture	3rd day	5th day	Total	3rd day	5th day	Total
23. x. 23	Control A	12·8	4·6	88·6	95	3	87	95
	A 1	11·71	22	93	96	7·5	84	91
	A 2	—	10·6	92·6	96	—	—	—
	A 3	—	16·3	95	98	—	—	—
	Control B	12·33	19	90	97	3·5	80	94
	B 1	11·84	37	96	97	32	95	98
	B 2	—	10·6	87	95	—	—	—
	B 3	—	31·3	92	93	—	—	—
	Control C	12·68	24	96	92	1·5	76	90
	C 1	11·80	40	87	91	1·5	86·5	93
	C 2	—	47	92	93	—	—	—
	C 3	—	31	95·6	98	—	—	—

II. The Effect of Drying Unafter-ripened Seed upon subsequent Growth—Grey Winter Oats.

Harlan and Pope (11), working with barley, have shown that the state of maturity not only affects the weight of the grain and germination but also the growth of the seedlings. From the treated and control samples "Firsts" (basal flower of spikelet) were grown in garden soil[1] in boxes of 100, each grain being spaced 2 inches apart in rows 2 inches distant. The seed was sown at a depth of half an inch on October 23rd,

[1] For soil analysis see Appendix.

1923, and the boxes placed in a large cool greenhouse. Equal watering conditions prevailed. The results obtained are set out in Table IV.

Table IV.

Growth of Control and Treated Samples of Selected Grain ("firsts").

Sample	% germination. Soil germin. visible shoots		Heights (correlation coefficient height and leaf area, $R = \cdot 81 \pm \cdot 02$)				Dry weights—7 weeks ol		
	9 days	14 days	No. of plants measured	Average height mms. 17 days	No. of plants measured	Average height mms. 30 days	No. of readings each 20 seedlings	Average dry weight 20 seedlings	ter co =
Control A	19·6	93	277	$29 \cdot 12 \pm \cdot 67$	297	$55 \cdot 3 \pm \cdot 61$	13	$\cdot 610 \pm \cdot 0062$	[illegible]
A 1	38	97	279	$38 \cdot 81 \pm \cdot 72$	296	$63 \cdot 4 \pm \cdot 77$	14	$\cdot 639 \pm \cdot 0047$	[illegible]
Control B	32	96	96	$39 \cdot 28 \pm \cdot 82$	295	$65 \cdot 7 \pm \cdot 54$*	13	$\cdot 571 \pm \cdot 0029$	[illegible]
B 1	57	97	98	$44 \cdot 01 \pm \cdot 78$	296	$66 \cdot 7 \pm \cdot 42$*	14	$\cdot 606 \pm \cdot 0043$	[illegible]
Control C	63	91	—	—	169	$68 \cdot 3 \pm \cdot 75$*	9	$\cdot 572 \pm \cdot 006$	[illegible]
C 1	70	92	—	—	172	$69 \cdot 25 \pm \cdot 65$*	9	$\cdot 610 \pm \cdot 0013$	[illegible]

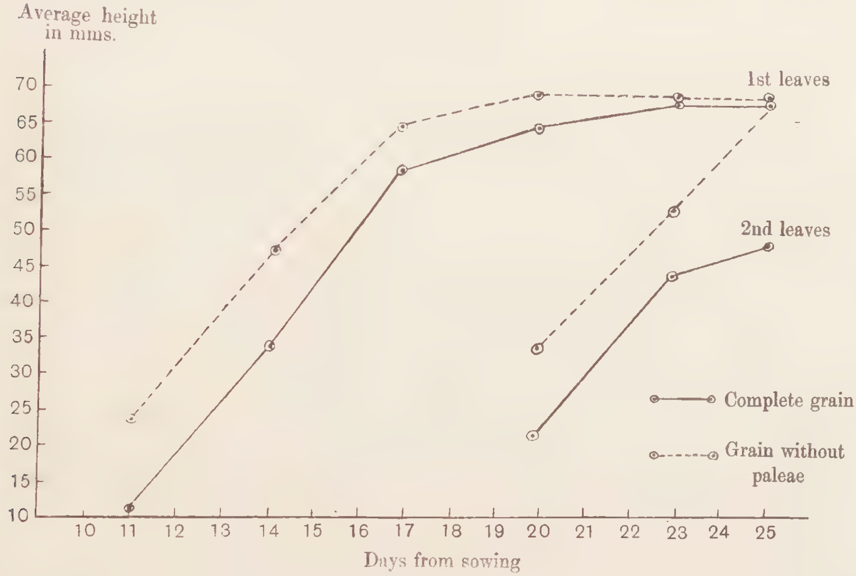
* Height of first leaf of control and treated equal, second leaf showing difference between control and treated plants.

Table IV shows that the earlier soil germination counts (9 days) confirm the sand tests in that the treated grains germinate quicker; they produce leaves which are taller at 17 days, later, however, the first leaves are equal but the second leaves showed a difference. A correlation coefficient, worked out on 120 seedlings, showed that the leaf area was closely correlated with the total height ($R = \cdot 81$). When the plants were carefully lifted, washed, dried and weighed, it was found that the treated plants were slightly heavier at 7 weeks. This series of experiments forms a concrete example of an increase in rate of germination being followed by increased vigour of seedling growth. Kondo (15) working with rice has obtained similar results, showing that ripe grains not only germinate faster but also grow better than do immature grains and the seedlings raised from them.

III. The Effect of Husk Removal on the Growth of the Seedlings—Ceirch du Bach Oats.

A pure line of Ceirch du Bach obtained from the Welsh Plant Breeding Station, possessing a high percentage of husk, was found to show a marked acceleration (72 per cent. on third day) of germination upon husk removal. From this well after-ripened sample, grain equal in size, weight and position on the parent plant were selected and sown, spaced in boxes, to compare the growth of seedlings from carefully

shelled grain[1] with that of control seedlings. The soil germination counts confirmed the sand tests, the shelled grain germinating quicker. The heights of the first leaves were measured at intervals of two or three days, and it was seen that the shelled grain seedlings maintained their initial advantage until their first leaves reached a maximum height which was later reached by the control seedlings; the second leaves however now showed a difference between "shelled" and control (see



Graph. Growth of seedlings from complete grain and grain with paleae removed—1st and 2nd leaves.

Graph). After a month the seedlings were removed and their dry weight obtained; on making allowance for the husk in control samples, it was seen that the shelled grain had produced slightly heavier plants. Treating growth as a process of accumulation by the compound interest system (2) the initial dry weights, and the period of growth being approximately equal the rate of interest (or efficiency index) is higher in the case of the shelled grain. The fact remains, however, that the period of actual photosynthesis was not known, and that but very small

[1] In these experiments the oats were carefully shelled by hand. Loveday and Stapledon (20) have shown that shelled grain in commercial samples is often injured and consequently gives low germination. Overgaard (18) has shown that such grain gives poor growth but that carefully shelled grain (when mixed with normal grain) gives good growth.

increases over the initial dry weight had been produced. The results obtained are set out in Table V.

Table V.

Husk Removal and Seedling Growth—Ceirch du Bach Oats.

% germination

Control			"Shelled"		
3rd day	5th day	Total	3rd day	5th day	Total
2	76	97	74	89	98

Heights

No. of days	Measured No. of plants	Average height 1st leaf control mm.	Average height 1st leaf "shelled" mm.	Average height 2nd leaf control mm.	Average height 2nd leaf "shelled" mm.
11	50	11·15 ± ·46	23·78 ± ·57	—	—
14	51	33·1 ± ·55	48·3 ± ·66	–	—
17	50	56·4 ± ·75	65·3 ± ·78	—	—
20	48	65·0 ± ·50	69·27 ± ·77	25·6 ± ·66	32·9 ± 0·81
23	50	68·0 ± ·58	69·27 ± ·69	46·1 ± ·76	54·2 ± 1·0
25	51	68·8 ± ·62	69·3 ± ·79	48·4 ± ·84	68·8 ± 1·1

Dry weight—month

Average dry weight of 100 plants			No. of batches weighed
Grain	Control seedlings	"Shelled" grain seedlings	
1·2055 caryopsis, ·545 husk	1·48 ± ·01	1·508 ± ·009	6

Having traced out the initial stages of growth and seen that husk removal produces not only an acceleration of germination in sand and soil, but also gives quicker leaf formation, an experiment to test the length of time that this effect could be observed was set up.

Equal grain of the same pure line of Ceirch du Bach oats was again employed. Thirty replications of pot cultures were employed for each early growth stage. Equal water, soil and light conditions prevailed for the two series—control and shelled grain. At different stages of growth, readings of heights were made before the plants were removed for immediate leaf-area determinations and subsequent washing and drying and weighing. The results obtained are shown in Tables VI and VII, the figures in brackets are those of the shelled grain placed below the control figures for direct comparison. It is seen that the earlier germination of the shelled grain causes larger leaf formation at 2, 3 and 4 weeks.

Table VI.

Growth of Plants from Complete and Shelled Grain. 1921 Seed—Ceirch du Bach (Pure Line) Oats. Selected Grain (firsts) sown.

(Figures in brackets are those of the Shelled Grain.)

I. Age, weeks	II. Number of plants		III. Average height*, mm. (or cm.)	IV. Average leaf area, sq. cm.	V. Average dry wt. per 100 plants, gm.	VI. Number of tillers	VII. $\frac{\text{Increase}}{\text{start}} \times 100$ $\frac{W2 - W1}{W1} \times 100$ Dry wt.	VIII. Weekly unit leaf rate $\frac{W2 - W1}{\frac{L1 + L2}{2}}$ (mg. per sq. cm.)		
			mm.		Seed:					
2	150		39·0 ± 0·95	·75	1·7505 complete		—		—	
			(46·2 ± 0·84)	(·90)	1·2055 husk off	—	—		—	
					i.e. nett					
3	150	1	62·1 ± 0·58	2·00	—		—		—	
		1	(67·6 ± 0·59)	(2·30)	—		—		—	
		2†	26·4 ± 0·57	—	—		—		—	
		2†	(31·3 ± 0·57)	—	—		—		—	
								Period		Weekly average
4	50 (2 per pot),	1	65·8 ± 0·48	3·18 ± ·087	2·555 ± ·081	—	66·7	For 1st 4 weeks	5·06‡	1·26‡
		2†	50·2 ± 0·67	-	2·01 nett	—	—			
		1	(70·1 ± 1·08)	(3·43 ± ·076)	(2·23 ± ·08)	—	(84·9)	,,	(5·98)‡	(1·49)
		2†	(58·2 ± 0·98)	—	—	—	—			
6	50 (2 per pot)		—	10·88 ± ·24	7·185 ± ·16	—	452	4 6th week	6·58‡	3·29
			—	—	6·64 nett } weights	—	—		(6·45)‡	(3·25)
			—	(9·97 ± ·21)	(6·55 ± ·05) } equal	—	(445)	,,	7·39§	—
			—	—	—	—	—	,,	(7·04)§	—
9	30 (2 per pot)		13·3 ± ·17‖	—	37·30 ± 1·8	8·6 ± ·36	—		—	
			(13·45 ± ·21)	—	(43·10 ± 1·7)	(9·9 ± ·24)	—		—	
			cm.							

* To leaf tip, fully extended. † 1st and 2nd leaf measured. ‡ Area calculated on linear basis.

§ Also calculated on exponential basis. $(\log_e L2 - \log_e L1)\,\frac{W2 - W1}{L2 - L1}$.

‖ Three tallest tillers per plant averaged for height.

Table VII.

Growth of Plants from Complete and Shelled Grain. 1922 Seed—Ceirch du Bach (Pure Line) Oats.
Selected Grain (equal firsts) sown.

(Figures in brackets are those of Shelled Grain.)

I. Age, weeks	II. Number of plants		III. Average height*, mm. (or cm.)	IV. Average leaf area, sq. cm.	V. Average dry wt. per 100 plants, gm.	VI. Number of tillers	VII. $\frac{\text{Increase}}{\text{start}} \times 100$ $\frac{W2 - W1}{W1} \times 100$ Dry wt.	VIII. Weekly unit leaf rate $\frac{W2 - W1}{\frac{L1 + L2}{2}}$ (mg. per sq. cm.) Period		Weekly average
			mm.		Seed:					
2	150		43·1 ± 0·74	·80	2·357 complete	—	—		—	
			(55·2 ± 0·41)	(1·40)	1·682 husk off	—	—		—	
					i.e. nett					
3	150	1	67·3 ± 0·42	2·30	—	—	—		—	
		2†	29·0 ± 0·52	—	—	—	—		—	
		1	(80·1 ± 0·47)	(3·20)	—	—	—		—	
		2†	(38·6 ± 0·66)	—	—	—	—		—	
4	50 (2 per pot)	1	70·3 ± 0·57	3·14 ± ·064	3·342 ± ·081	—	59	For 1st 4 weeks	6·27‡	1·57
		2†	58·9 ± 0·57	—	2·667 nett	—	—			
		1	(83·7 ± 0·67)	(3·81 ± ·054)	(2·86 ± ·022)	—	(70)	,,	(6·18)‡	(1·54)
		2†	(70·9 ± 0·81)	—	—	—	—			
6	50 (2 per pot)		—	10·28 ± ·28	8·15 ± ·17	—	344	4–6th week	7·16‡	3·58
			—	—	7·475 nett	—	—		(8·56)‡	(4·28)
			—	(11·72 ± ·24)	(9·50 ± ·17)	—	(465)	,,	7·98§	
			—	—	—	—	—	,,	(9·43)§	
9	30 (2 per pot)		12·18 ± ·23‖	—	38·12 ± 2·34	5·9 ± ·12	equal in ht. and wt.		—	
			—	—	37·44 nett				—	
			(12·18 ± ·19) cm.	—	(38·14 ± 1·01)	(6·76 ± ·14)			—	

* To leaf tip, fully extended. † 1st and 2nd leaf measured. ‡ Area calculated on linear basis.

§ Also calculated on exponential basis. $(\log_e L2 - \log_e L1) \frac{W2 - W1}{L2 - L1}$.

‖ Three tallest tillers per plant averaged for height.

With 1922 seed the relative increase in weight at 4 weeks is 59 per cent. for complete grain and 71 per cent. for shelled grain. The leaf areas and weights are in favour of the shelled grain at 6 weeks. At 9 weeks an advantage remains with the shelled grain in tillering—8·6—control, 9·9 shelled grain. At 11 weeks, unfortunately, the roots of the series had begun to reach the bottom of the largest Doulton pots so that further data were not obtained. Considering the efficiency of the leaves as measured by the unit-leaf-rate (3) the 1922 grain produce more efficient leaves than the 1921 seed.

IV. The Effect of Soaking the Seed upon Germination and subsequent Growth—Grey winter Oats and Standard Red Wheat.

To test the effect of soaking upon growth, a pure line of Grey Winter Oats, well ripened and matured, was used; equal grain being selected. Soaking took place for 24 hours, at the rate of 10 gm. seeds per 100 gm. of water at 14° C. The grain was sown in boxes in spaced rows. Both control and soaked samples were sown in normal garden soil possessing a normal water supply. Table VIII shows the results obtained.

Table VIII.

Growth of Soaked and Control Seed.

Sown 22. x. 23.

	Control		Soaked		Germination		
Age	No. of plants	Average height in mm. 1st leaf	No. of plants	Average height in mm. 1st leaf	Soaked	Control	
Days					Sand	Sand	
14	58	20·74 ± ·792 (*a*)	60	33·18 ± ·729 (*a*)	34 %	3rd day	0
	56	25·43 ± ·748 (*b*)	58	39·4 ± ·929 (*b*)	93 %	5th day	25
	58	23·37 ± ·671 (*c*)	56	30·97 ± ·758 (*c*)	98 %	Total	91
					Soil	Soil	
20	60	59·92 ± ·897 (*a*)	60	73·98 ± ·861 (*a*)	54 %	11 days	35 %
					No. of visible shoots		
	49	63·83 ± 1·14 (*b*)	59	77·9 ± 1·11 (*b*)			
	60	64·40 ± 1·03 (*c*)	58	68·4 ± ·589 (*c*)			
		Dry weights per 100		Dry weights per 100			
Weeks							
6	60	3·00 ± ·019 (*a*)	60	3·32 ± ·032 (*a*)			
	56	3·05 ± ·085 (*b*)	59	3·29 ± ·032 (*b*)			
	60	3·06 ± ·061 (*c*)	59	3·29 ± ·037 (*c*)			
Average		3·036		3·30			
		Control = 100		In terms of Control 109			

During the cold autumn weather little growth was possible but it is clear from the above table that this treatment has not only hastened germination, but has also accelerated seedling growth. Many other workers have obtained increased growth by soaking (see Kidd and West's summary of this literature).

Kraus and Wollny (21) working on the effect of soaking upon subsequent growth and yield pointed out the importance of the conditions prevailing at the time of soaking, and they obtained beneficial results when using the minimum of water. Kidd and West suggest that soaking in small volumes of water permits of free gaseous interchange. To test the effect of soaking in the presence of excess oxygen and carbon dioxide samples of Black Bell III Oats were soaked in saturated solutions of these gases at 14° C. for 6 hours. Treated grain of equal weight ("firsts" only) were grown in replicated rows of 5 feet, alongside control and water soaked seed. On weighing the plants after 7 weeks, whilst soaking had again caused increased growth, no marked advantage was obtained by soaking in the presence of excess oxygen nor was a marked retardation of growth produced by the carbon dioxide soaking treatment. Exactly similar treatments were carried out with a sample of wheat, Standard Red; the results are shown in Table IX.

Table IX.

Germination and Growth of Wheat—Various Seed Treatments.

	Control	Seed soaked in tap water	Soaked in oxygen saturated water	Soaked in carbon dioxide saturated water
Germination:				
Sand, 3rd day	43 %	51 %	53 %	55 %
Total	84 %	84 %	79 %	78 %
Soil, 9 days. No. of visible shoots	58 %	55 %	59 %	64 %
Total established	66 %	66 %	66 %	60 %
Dry weights of 100 plants, 6 weeks	36·1 ± ·43	38·2 ± ·47	37·6 ± ·68	34·1 ± ·73
In terms of control	100	106	104	94
No. of plants weighed	350	350	400	375

It is seen that soaking wheat in water has produced a beneficial effect on germination and growth as in oats, but by soaking in the presence of excess carbon dioxide, any benefit derived from ordinary soaking has been obliterated and the resulting plants are even lighter than the non-soaked controls. Moreover, a number of seedlings from carbon dioxide soaked grain died off after germination. It is noteworthy

that no indication was given by the sand germination tests of this harmful effect in the case of wheat.

Further trials were carried out with Cook's Wonder Wheat, the following "oxidising" treatments being employed:

(*a*) Soaking for 18 hours in weak hydrogen peroxide, ·56 volume, due to the catalase reaction slow bubbling took place all the time. 15° C.

(*b*) Soaking in 2 per cent. permanganate solution, which chars and weakens the outer coat of the grain, at 15° C.

(*c*) Ozonised oxygen from an ozoniser was passed into the soaking water before placing the seeds in it, and continued for 6 hours; after an interval of 10 hours again passed through for 2 hours. 15° C. (per cent. of ozone, 4).

(*d*) Water soaking for 18 hours. In all cases the rate of soaking was 10 gm. of grain per 100 gm. of water. 15° C.

Eight replications were sown in rows 5 feet long, spaced 9 inches apart, sown at the rate of 2 per inch, half an inch depth, on April 1st, 1924. The results of the growth made by the seedlings are given in Table X along with germination test figures.

Table X.

Wheat. "Oxidation" Treatments of Grain. Cook's Wonder Wheat.

Treatment	I. Sand germination test: No. germ. on 3rd day	II. Sand germination test: % germ. [illegible]th day	III. Total germination	IV. % above soil, 3 weeks	V. % established, 6 weeks	VI. Av. dry wt. per row	VII. 6 weeks old. Av. dry wt. per 100 plants	VIII. 9 weeks dry wt. per row. 'Tops' only	IX. 9 weeks dry wt. per 100 'tops' plants	X. No. of tillers per row, 9 weeks	XI. Av. no. tillers per plant, 9 weeks
Control	1	96	97	75	82	63·9 (=100)*	63·9 ±0·90 (=100)	35·4 (=100)	36·48±0·81 (=100)	170	1·76 (=100)
Soaked in $KMnO_4$ 2 %, 50 gm. in 250 c.c. for 18 hours at 15° C.	1	78	100	83·6	82	76·36 (119)	76·36±·52 (119)	41·2 (116)	41·24±1·2 (113)	188	1·89 (107)
Soaked in 4 % ozone and oxygen saturated solution at 15° C.	37	93	94	83·1	89	81·75 (128)	76·4 ±1·4 (119)	43·59 (123)	40·22±1·2 (110)	205	1·89 (107)
Soaked for 18 hours in hydrogen peroxide, ·56 vols., at 15° C.	0	58	64	58·5	59	47·4 (74)	66·27±0·43 (103)	32·29 (91)	41·5 ±0·71 (113)	160	2·04 (115)
Soaked in distilled water for 18 hours at 15° C.	26	96	97	80·6	83·4	71·42 (111)	71·42±0·82 (111)	44·95 (127)	42·31±0·89 (117)	207	1·96 (111)

* Figures in brackets are for comparison with the control (at 100) in this and subsequent tables.

The following conclusions are drawn from the preceding table:

Hydrogen Peroxide. The toxic action of hydrogen peroxide even in a weak solution (·56 volume) is shown by the reduction in the number of germinations at 3 and 5 days and in the total germinations. At 6 weeks plants produced from hydrogen peroxide soaked seeds are poorer than those from seed soaked in water. At nine weeks the better spacing conditions these plants enjoyed, begins to show its effect.

Potassium Permanganate. The treated grain, despite their black appearance, germinated, though not as quickly as grain soaked in water. At 6 weeks the plants raised from permanganate soaked seeds were heavier than those from seed soaked in water. At 9 weeks no difference was detected between the weight of the tops of plants from permanganate soaked seed and those from seed soaked in water.

Oxygen and Ozone treated seed. These seeds germinated very quickly as compared with seed soaked in distilled water. At 6 weeks the produce from such seeds was heavier than that from control or water soaked seed. At 9 weeks, however, though still heavier than the control plants they were not heavier than plants raised from seed soaked in water. The "ozone and oxygen treatment" produced a different effect from the hydrogen peroxide treatment.

These experiments were repeated with a very old sample of "Standard Red" wheat. The hydrogen peroxide killed the seeds outright. The permanganate solution reduced the number of seedlings established considerably. The "oxygen and ozone" treatment increased the number of seedlings established, as did the distilled water treatment. The rows were so irregular and poor as to make weight comparisons worthless.

V. The Effect of Soaking the Seed upon the Germination and Growth of Various Species of Grasses.

Selected samples showing very poor "energy" and total germination were soaked for 10 hours in small quantities of water, the seed was only just covered. Air drying on blotting paper for 20 hours followed, so that the small seeds could be sown separately at the rate of 100 per box. The boxes were placed out in the open after the young shoots were up.

From the following table it is seen that the number of germinations was increased by soaking. The total weight of the plants produced was increased. The average weight per 100 was also increased for Perennial Rye Grass, Timothy and Fine Leaved Fescue. These Cocksfoot results were inconclusive. The experiment was, therefore, repeated in the autumn

Table XI.

Effect of Soaking Grass Seeds upon Germination and Seedling growth —Preliminary Trial.

5 weeks {Sown, 29. vi. Harvested, 3. viii.

Species	Control: Established seedlings %	Control: Average dry weight per 100 gm.	Soaked: Established seedlings %	Soaked: Average dry weight per 100 gm.	Percentage increase in dry weight
Perennial Rye Grass	20	13·78	23	17·33	26
Timothy	49·5	5·13	56	5·32	4
Fine Leaved Fescue (New Zealand)	44	1·43	40	1·92	35
Cocksfoot*	57	—	65·5	—	2

* Replications did not agree—one showing slight increase in dry weight, the other slight decrease.

on a larger scale, using besides the above samples further samples of Cocksfoot freshly harvested. Seed was soaked for 24 hours, 5 gm. of seed in 500 c.c. water. The seed was sown at the rate of 200 per box at 1-inch intervals in rows also 1 inch apart, and was covered equally by moist soil; all boxes were watered 12 hours after sowing for the first time, and placed in a large unheated greenhouse. Copenhagen tank germination tests, soil germination counts and dry weight determinations (at 8 weeks) were carried out; the results are shown in Table XIII. Twenty seedlings were weighed together as a unit.

Table XII.

Effect of Soaking Grass Seed upon Seedling Growth.

Species and sample	Soil germination counts: Control 17 days	Control 24 days	Soaked 17 days	Soaked 24 days	Dry weights, 2 months: No. of plants	Av. dry wt. per 100. Control. gm.	No. of plants	Av. dry wt. per 100. Soaked gm.	Increase % over control (=100)
Timothy (an old sample)	52	64	53	68	(a)* 120	·347 ±·008	100	·430±·005	24
,, (the same sample)					(b)* 140	·251 ±·007	120	·302±·0047	20
Fine Leaved Fescue (New Zealand)	10	23	16	30	20	·0871	30	·1156	32
Cocksfoot (an old sample)	42	62	47	63	(a)* 120	·5325±·0038	120	·625±·0016	17
,, (the same sample)					(b)* 140	·4965±·0087	140	·585±·009	18
New sample (1), Cocksfoot	34	69	49	61	260	·475 ±·002	240	·585±·003	23
New sample (2), Cocksfoot	39	60	60	75	260	·480 ±·004	260	·550±·0015	17

* A duplicate series of same seed sample grown under different light conditions with duplicated controls.

From the preceding Table it is seen that after 8 weeks' growth in autumnal conditions, an increase in dry weight, of approximately 20 per cent. over the control plants, has been produced by soaking the seed of Timothy, Fine Leaved Fescue and Cocksfoot, for 24 hours in excess of water.

The experiments previously described were carried out in boxes and the seed carefully spaced. A further series of trials were carried out with the grass seed treatments, in which the plants were grown in rows in a bird-proof cage. An estimation of the effect of seed treatment upon yield of herbage was attempted. Indigenous and commercial samples were subjected to the various treatments. Soaking in weak permanganate solution was tried because indications had been obtained that such a solution disorganised the outside covering of the caryopsis. The seed was sown, 100 per row 5 feet long, six replications of each treatment and control, on May 14th, 1924. The top growth was estimated 3 months later by clipping the plants to ground level and weighing the produce after drying.

Table XIII.

Cocksfoot. Seed Treatment and Growth.

	I. % soil germin. 9 days	II. % germin. 2 weeks	III. Notes. 5 weeks	IV. Av. yield per row "tops" dry wt. gm. 12 weeks	V. Av. yield per 100 plants "tops" dry wt. gm. 12 weeks
			Indigenous sample Bc 225/1.		
Control	2·0	31·0	Much thinner than all treated. In order of merit—4th	11·55 ± 0·92 (100)	37·3 (100)
Heated for 48 hrs. at 40° C.	2·5	46·0	Better than control. 3rd in order of merit	16·68 ± 1·1 (143)	36·2 (97)
Soaked in 1 % $KMnO_4$ solution for 47 hrs. (2·5 gm. seed in 250 c.c.)	8·3	59·0	Nearly as good as soaked in water. 2nd in order of merit	19·35 ± 0·86 (166)	32·7 (87)
Soaked in distilled water for 48 hrs. (2·5 gm. in 250 c.c.)	7·3	59·0	Best rows—all replications	21·01 ± 1·4 (180)	35·5 (95)
			Commercial sample Bc 1591.		
Control	2·2	36·6	Rows not so good as any of treated	18·8 ± 0·82 (100)	51·0
Heated for 48 hrs. at 40° C.	3·3	44·0	Better than control, slightly	18·3 ± 1·1 (97)	41·0
Soaked in 1 % $KMnO_4$ solution for 47 hrs. (2·5 gm. seed in 250 c.c.)	12·3	54·3	Better than control, and heated rows	23·46 ± 1·2 (124)	43·0
Soaked in distilled water for 48 hrs. (2·5 gm. in 250 c.c.)	17·8	55·0	Appeared the best rows	22·9 ± 0·89 (122)	44·0

Table XIV.

Meadow Fescue. Seed Treatment and Growth.

	I. % soil germin. 9 days	II. % germin. 2 weeks	III. Notes. 5 weeks	IV. Av. yield per row "tops" dry wt. gm. 12 weeks	V. Av. yield per 100 plants "tops" dry wt. gm. 12 weeks
		Indigenous sample Bf 15/1.			
Control	3·6	45·4	Did not show much difference between treatments	10·6 ±1·1	23·0 (100)
Heated for 48 hrs. at 40° C.	4·6	45·4	Equal with soaked	10·2 ±0·50	23·0 (100)
Soaked in 1 % $KMnO_4$ solution for 47 hrs.	3·1	40·4	Plants slightly better than rest of treatments	11·8 ±0·66	27·1 (117)
Soaked in distilled water for 48 hrs. (2·5 gm. in 250 c.c.)	5·0	43·0	Not quite as good as some controls	11·6 ±0·11	28·7 (124·6)
		Commercial sample Bf 26.			
Control	12·7	69·8	All very much alike	19·5 ±0·83 (100)	27·6 (100)
Heated for 48 hrs. at 40° C.	12·7	76·4	All very much alike	18·51±0·67 (95)	24·3 (89)
Soaked in 1 % $KMnO_4$ solution for 47 hrs.	45·0	76·2	All very much alike	23·5 ±0·56 (120)	30·7 (111)
Soaked in distilled water for 48 hrs. (2·5 gm. in 250 c.c.)	53·0	80·6	Slightly better than the rest	23·26±1·1 (118)	28·6 (103·5)

Table XV.

Tall Fescue. Seed Treatment and Growth.

	I. % soil germin. 9 days. Visible shoots	II. % germin. 2 weeks	III. Notes, 5 weeks	IV. Av yield per row "tops" dry wt. gm. 12 weeks	V. Av. yield per 100 plants "tops" dry wt. gm. 12 weeks
		Indigenous sample Bn 19/1.			
Control	2·7	47	Control rows made fairly good growth	15·15±0·74 (100)	32·3 ±1·9 (100)
Heated for 48 hrs. at 40° C.	5·0	47	Not so good as control	17·26±0·74 (114)	36·4 ±2·2 (112)
Soaked in 1 % $KMnO_4$ solution for 47 hrs.	4·7	54	Not so good as control	17·46±1·06 (115)	33·7 ±3·0 (104)
Soaked in distilled water for 48 hrs. (2·5 gm. in 250 c.c.)	6·8	59	Slightly better than control	19·9 ±0·5 (131)	35·92±2·3 (111)
		Commercial sample Bn 40.			
Control	6·8	61	Control rows fairly good	19·26±1·3 (100)	30·9 ±1·6 (100)
Heated for 48 hrs. at 40° C.	6·1	67	Slightly better than control	18·27±1·3 (95)	29·3 ±1·1 (95)
Soaked in 1 % $KMnO_4$ solution for 47 hrs.	41·0	69·5	Slightly better than control	23·5 ±0·8 (122)	34·01±1·0 (110)
Soaked in distilled water for 48 hrs. (2·5 gm. in 250 c.c.)	40·0	66	Distinctly better than control	24·87±1·4 (129)	38·9 ±2·4 (126)

Table XVI.

Perennial Rye Grass. Seed Treatment and Growth.

	I. % soil germin. 9 days. Visible shoots	II. % germin. 2 weeks	III. Notes, 5 weeks	IV. Av. yield per row "tops" dry wt. gm. 12 weeks	V. Av. yield per 100 plants "tops" dry wt. gm. 12 weeks
			Indigenous sample 25/1.		
Control	51·5	73	All control rows made good growth	39·75 ± 1·4 (100)	49·59 ± 1·6 (100)
Heated for 48 hrs. at 40° C.	44·0	78	Not quite as good as control	36·4 ± 1·0 (91)	46·69 ± 1·9 (94)
Soaked in 1 % $KMnO_4$ solution for 47 hrs.	43·1	69	Not quite as good as control	34·58 ± 1·8 (87)	44·6 ± 2·2 (89)
Soaked in distilled water for 48 hrs. (2·5 gm. in 250 c.c.)	58·5	76	Better than control	41·4 ± 1·3 (104)	56·7 ± 3·8 (114)
			Commercial sample Ba 1352.		
Control	40·9	84	Control rows made good growth	38·55 ± 1·4 (100)	52·9 ± 1·9 (100)
Heated for 48 hrs. at 40° C.	37·2	86	Not as good as control	36·83 ± 1·1	47·8 ± 1·7 (90)
Soaked in 1 % $KMnO_4$ solution for 47 hrs.	33·3	76	Poorer than control	31·9 ± 0·68 (83)	46·8 ± 2·2 (88)
Soaked in distilled water for 48 hrs. (2·5 gm. in 250 c.c.)	60·5	78	All much better than control	41·99 ± 0·50 (108)	55·1 ± 2·8 (104)

Cocksfoot Indigenous. By soaking in distilled water and in 1 per cent. $KMnO_4$ an increase in germination ("energy" and total) figures has been produced. Heating the seed also improved germination—though to a less extent than soaking. When the tops were cut, three months after sowing, the yield obtained from equal sowing per row shows the beneficial effect of the seed treatments, a gain of as much as 80 per cent. over the control being produced by soaking. This increase in yield was due to the greater number of plants established for the weight per 100 plants was almost constant for all the series. There can be little doubt that the space factor has entered considerably into the yield per 100 plants. It is to be noted that the treated plants have yielded nearly as well as the control plants, which, by reason of their poorer germination possessed more space.

The germination of the commercial sample was improved by the treatments. The total yield obtained was improved by soaking, but the

weight per 100 plants of the control plants was greater than that of the treated owing to the spacing conditions that resulted. The commercial sample generally out-yielded the indigenous in weight per 100 plants and in weight per row at the commencement of growth—for the first three months.

Meadow Fescue. Soaking indigenous seed in water or $KMnO_4$ solution had very little effect upon the soil germination—either rate or total. An increase in weight per 100 plants was produced by these treatments. By soaking the commercial sample, an increase of 36 per cent. was produced in the 9 days' soil germination (visible shoots) and the final germination figures were higher for the treated plants than for the control. Soaking increased by approximately 20 per cent. the weight per row at 3 months, whilst the weight per 100 plants was also increased slightly. The control commercial seed gave more top growth than the indigenous control seed. There was, however, little difference between the two soaked samples.

Tall Fescue. The various treatments produced little effect upon the rate of germination, but soaking in water increased the number of plants established of the indigenous sample. For this reason, the yield per row was increased by soaking the seed. The errors on the weight per 100 plants were too large to permit comparisons being made.

Soaking in both $KMnO_4$ and water greatly accelerated germination —40 per cent. of the soaked seed had germinated in 9 days and 7 per cent. of the control seed of a commercial sample. A slight increase in the number of established plants was produced by soaking. The yield per row was increased by soaking the seed in water and in permanganate, whilst the weight per 100 plants was also increased by soaking in water. No great difference in the growth of commercial and indigenous samples was observed with this species.

Perennial Rye Grass. Indigenous. Heating and soaking in permanganate solution decreased the rate of germination, whilst soaking in water slightly increased the rate of germination. Heating, and soaking in permanganate caused a slight reduction in the weight per row and the weight per 100 plants, whilst soaking in water caused a slight increase in the yields per row and per 100 plants. Very similar results were obtained with a commercial sample, but a more marked increase in the rate of germination was produced by soaking with the commercial sample. There was no great difference between the growth of the indigenous and commercial samples as in the case of the Cocksfoot samples.

Although uneven germination gave rise to unequal spacing conditions which masked in some cases the effects of the seed treatments, yet the results for all the samples taken together, show that soaking in water has a beneficial effect upon the yield per plant, besides hastening germination. The permanganate treatment considered for all the samples has produced no marked effects upon yield. Unlike the oats, which benefited by the heating treatment (previously described in Part I) the grass samples were not freshly harvested seed, and no beneficial or harmful effect of any magnitude has been produced by this treatment. The most striking difference between the growth of commercial and indigenous samples is shown by Cocksfoot where the indigenous type grows less rapidly.

VI. The Effect of Soaking the Seed upon Germination and Growth of some Economic Leguminoseae.

Experiments with a few species of Leguminoseae were carried out. The effect of soaking for 12 hours and for 24 hours at temperatures of 14° and 24° C. was investigated. The seed was soaked at the rate of 10 gm. per 100 c.c. of water in germination saucers, there being about half an inch of water covering the seed when swollen. The seed was sown within 2 hours of removal from water; 12 seeds were sown per large pot, six replications of control and each treatment were made. An equal mass of soil, to give equal depth of sowing, was used to cover the seeds and all the pots were watered equally after sowing. Sand germinations were set up at the same time. Some analysis of the growth made in 6 weeks was attempted; for this, all the roots were carefully removed (the soil being powdered very carefully). The whole plants were washed, dried at 100° C. and weighed.

Table XVII shows the results for peas ("Little Marvel"—Sutton's), after 6 weeks' growth from October 17th, 1923, in a large unheated greenhouse. It is seen that the soaked seed sprouted earlier in sand and appeared earlier through the soil, soaking for the longer periods did not steadily reduce the germination. A slight increase in the top growth was produced by soaking for 12 hours, but the percentage of root and seed remains together was slightly lower in the case of the soaked seed. A small reduction in the yield per 100 plants was obtained, but these figures gave differences that were barely significant. Kidd and West (14) by growing peas on sand found that soaking definitely reduced the length of the root produced, but a slight increase in the height of the top growth over that of control seed was noticed in the case of seed

soaked for 24 hours. The results are then in general agreement but the periods of soaking which caused the differences varied, being 12 hours in this experiment and 24 hours in Kidd and West's.

Table XVII.

Peas. Six weeks old. Winter Growth.

I. Series	II. No. of soil plants	III. Percent. established	IV. Soil 10 days. Visible shoots %	V. Sand germ. "energy", 3 days %	VI. Sand total %	VII. Yield obtained from equal no. of seeds gm.	VIII. Dry wt. yield per 100 plants gm.	IX. Dry wt. "tops" only 100 plants gm.	X. Roots and cotyledons per 100 plants. Difference VIII and IX	XI. Percent. roots and seed remain	XII Percent. tops
Control	67	95	40	33	92	11·47 (100)	17·11 ± ·42 (100)	6·71 ± ·1 (100)	10·40 (100)	60·7	39·3
Soaked for 12 hours at 14° C.	63	87·5	72	88	94	10·31 (89·9)	16·36 ± ·30 (95·6)	7·31 ± ·31 (108)	9·05 (86·9)	55·21	44·78
Soaked for 12 hours at 24° C.	67	95	71	89	93	11·19 (97·5)	16·69 ± ·61 (97·5)	7·46 ± ·31 (111)	9·23 (88·7)	55·3	44·7
Soaked for 24 hours at 14° C.	66	94	68	94	94	10·46 (91·1)	15·84 ± ·36 (92·6)	6·60 ± ·10 (98)	9·06 (87·0)	57·1	42·9
Soaked for 24 hours at 24° C.	61	84·7	80	91	96	9·84 (86·6)	16·12 ± ·51 (94·2)	6·78 ± ·23 (101)	9·52 (91·4)	59·0	41·0

A similar experiment was carried out in summer, the plants being spaced in short rows. Ten replications of each treatment and of the control were sown on May 16th, 1924. As the seed was not graded by weight the individual plants were somewhat uneven. A very heavy rainfall took place just after sowing was completed, which masked the effect of the treatments. The results shown in Table XVIII indicate that in the case of peas grown in conditions approximating to field conditions, pre-soaking has produced no appreciable effect upon growth when the crop yield was treated as a statistical result, moreover the treated and control replications appeared equal throughout the growth period.

Table XVIII.

"Pioneer" Peas. Summer Growth in Rows for 5 Weeks.

Treatment	I. No. of plants for data III, IV, V, VI	II. % soil germin. 12days. Visible shoots	III. Height in cm. 2 weeks	IV. Height in cm. 3 weeks	V. Average No. of leaflets, 3 weeks	VI. Height in cm. 5 weeks	VII. Dry weight 100 tops gm.
Control	45	94	2·58 ± ·039	4·86 ± ·095	6·5	15·86	36·67 ± 2·1
Soaked for 12 hours at 14° C.	41	84	2·63 ± ·054	4·58 ± ·14	6·7	15·2	36·09 ± 1·8
Soaked for 12 hours at 24° C.	47	95	2·69 ± ·052	4·55 ± ·097	6·9	15·5	36·22 ± 2·7
Soaked for 24 hours at 14° C.	45	87	2·61 ± ·06	4·64 ± ·12	6·3	15·4	31·71 ± 3·01
Soaked for 24 hours at 24° C	46	91	2·79 ± ·075	4·86 ± ·10	6·6	16·2	33·07 ± 1·3

Beans.

The results of the winter trial with pot-sown soaked and control seed are shown in Table XIX.

The final germination in sand and soil was not affected (steadily) by soaking—Columns III and VI. The rate of germination was greatly increased by soaking—counts of visible shoots in the case of soil-grown plants showing as much difference in the extreme case (control, and soaked for 24 hours at 24° C.) as 84 per cent., after 14 days.

The total yield was slightly increased by soaking for 24 hours; by soaking for 12 hours a yield equal to that of control was obtained. When the yield data was analysed, however, it was seen that much more top growth was made by the soaked plants. Column XI shows the heights of the different series, an increase of 52 per cent. being obtained by soaking for 24 hours at 24° C. A difference of 42 per cent. was obtained in the dry weight figures of the control and soaked for 24 hours at 24° C., "tops." Soaking for 12 hours produced a difference

Table XIX.

Beans. Sutton's "Prolific Longpod." Growth for 6 weeks—winter.

I. Series	II. No. of soil plants for data XI	III. Percent. established	IV. Percent. soil, 14 days. No. visible above soil	V. Percent. sand, 3 days. No. germin.	VI. Percent. sand. Total	VII. Actual yield from equal no. of seed gm.
Control	69	97	0	27	97	84·3
Soaked for 12 hours at 14° C.	69	97	42	31	95	85·27
Soaked for 12 hours at 24° C.	72	100	50	33	98	87·68
Soaked for 24 hours at 14° C.	64	91	69	40	96	84·98
Soaked for 24 hours at 24° C.	71	98	84	42	97	91·4

Series	VIII. Dry wt. yield per 100 plants gm.	IX. Dry wt. tops per 100 plants gm.	X. Dry wt. remains of seed only per 100 plants gm.*	XI. Height in cm. of tops	XII. Per-cent. tops	XIII. Per-cent. roots
Control	121·85 ± 4·5	42·85 ± 1·89 (100)	53·0 ± 1·64 (100)	8·8 ± ·32 (100)	35	21
Soaked for 12 hours at 14° C.	123·6 ± 3·9	54·70 ± 2·4 (128)	45·2 ± 2·69 (85)	11·14 ± ·41 (132)	45	19
Soaked for 12 hours at 24° C.	121·87 ± 4·3	51·07 ± 2·39 (120)	46·6 ± 2·0 (88)	10·77 ± ·25 (122)	42	20
Soaked for 24 hours at 14° C.	132·89 ± 3·7	58·67 ± 2·2 (137)	47·8 ± 1·49 (90)	12·12 ± ·22 (138)	44	20
Soaked for 24 hours at 24° C.	128·9 ± 3·6	60·85 ± 1·75 (142)	42·9 ± 2·6 (81)	13·38 ± ·43 (152)	47	19·5

* Dry matter in seed = 43·5 % of original dry wt. seed.

of approximately 25 per cent. in favour of the soaked seed (column IX). The percentage of true root remained remarkably steady for all series —approximately 20 per cent. (column XIII). On weighing the remains of the seed separately it was clearly seen that the increase made by soaked seeds over control seeds in "top" growth was made at the expense of the food stored in the seed (column X). Soaking had made the transference of food from cotyledons to shoot much more rapid.

The errors of the weight readings are too large to allow of any reliable comparisons between the effect of soaking at 14° and 24° C. being made on the dry weight per 100 tops. It was not improbable that soaking at different temperatures produced results which varied according to the length of the soaking period or, that soaking at a higher temperature did not always produce a more marked effect than soaking at a lower temperature. Readings of heights, however, allow some comparisons and show that soaking for 24 hours at 24° C. produced taller plants than soaking at 14° C. for the same period.

Growth took place in an autumn peculiar for the prolonged periods of cold weather that ensued. The plants were often subject to temperatures little above freezing point. For this reason, it is thought that little assimilation by the leaf could take place. Thus it is not surprising to find that there is no marked advantage in total weight, shown by the plants possessing more leafage and top growth. In fact, the final weights of the beans produced did not differ very much from the weight of the original seed. Given warmer conditions, there would be a marked increase over the control weights shown by these plants possessing a larger leaf area. Such results were obtained by other workers (Wollny (20)). In the case of beans, food transference and more rapid growth of the tops was brought about by soaking. Why rapid food transference to the roots should not be brought about to give a greater percentage of root does not seem clear unless it was that the soil temperature remained too low whereas the air temperature fluctuated and short warm periods favoured stem and leaf growth.

A summer field experiment using Giant Windsor variety of beans was also carried out. Ten replications of spaced seed were sown in rows, the seed was graded into large, medium and small—over 3 gm. large, 2–3 gm. medium, less than 2 gm. small, the weight of the mixed seed being 240·8 gm. per 100, having a moisture content of 15·8 per cent. The results are shown in Tables XX and XXI, for the three grades of seed weight separately.

It is seen that the rate of germination has been increased by soaking,

Table XX.

Beans. Sutton's "Giant Windsor." Growth 5 weeks. Summer. Medium Weight Seed.

I. Series	II. No. of visible shoots, 2 weeks %	III. Established %	IV. Height in cm. 3 weeks	V. No. of expanded leaflets, 3 weeks	VI. Height in cm. 5 weeks	VII. Average dry wt. per 100 tops, 5 weeks	VIII. Average dry wt. of 100 seed remains
Control	50	96	5·89 ± ·22 (100)	3·39 ± ·26 (100)	25·5 ± ·86 (100)	191·4 ± 5·1 (100)	31·6 ± 0·44 (100)
Soaked for 12 hrs. at 14° C.	56	100	6·16 ± ·13 (104·6)	3·86 ± ·10 (113)	28·3 ± ·82 (110)	204·4 ± 4·7 (106)	34·4 ± 0·91 (107)
Soaked for 12 hrs. at 24° C.	68	100	6·26 ± ·13 (106·3)	4·13 ± ·16 (122)	29·7 ± ·55 (116)	203·4 ± 5·4 (106)	32·02 ± 0·66 (101)
Soaked for 24 hrs. at 14° C.	72	98	7·29 ± ·17 (124)	4·12 ± ·16 (121)	30·37 ± ·51 (118)	208·4 ± 3·9 (109)	33·75 ± 0·43 (106)
Soaked for 24 hrs. at 24° C.	66	98	6·84 ± ·18 (116)	4·87 ± ·19 (143)	30·44 ± ·62 (119)	231·5 ± 7·9 (121)	32·57 ± 1·3 (103)

Table XXI.

Beans. Sutton's "Giant Windsor." Growth 5 weeks. Summer.

	Small seed				Large seed			
I. Series	II. Height in cm. 3 weeks	III. No. of expanded leaflets, 3 weeks	IV. Height in cm. 5 weeks	V. Dry wt. per 100 tops, gm.	VI. Height in cm. 3 weeks	VII. No. of expanded leaflets	VIII. Height in cm. 5 weeks	IX. Dry wt. per 100 tops
Control	4·66 ± ·25 (100)	3·3 ± ·19 (100)	23·9 ± 1·0 (100)	148·8 (100)	4·91 ± ·19 (100)	2·6 ± 1·16* (100)	30·1 ± ·81 (100)	242·0 (100)
Soaked for 12 hrs. at 14° C.	6·33 ± ·09 (135)	3·77 ± ·24 (114)	27·9 ± 0·80 (116)	174·9 (118)	—	—	—	—
Soaked for 12 hrs. at 24° C.	6·33 ± ·23 (135)	4·0 ± ·27 (121)	27·4 ± 0·94 (113)	173·8 (117)	6·8 ± ·16 (138)	4·90 ± 0·20 (188)	33·8 ± 1·3 (112)	286·5 (118)
Soaked for 24 hrs. at 14° C.	6·80 ± ·11 (145)	4·16 ± ·20 (123)	30·36 ± 0·68 (127)	189·1 (126)	—	—	—	—
Soaked for 24 hrs. at 24° C.	6·27 ± ·24 (133)	4·72 ± ·20 (141)	27·5 ± 0·91 (114)	166·0 (112)	5·98 ± ·19 (122)	4·98 ± 0·27 (190)	34·79 ± 1·3 (115)	281·3 (116)

* Very uneven.

though the total number of seedlings produced was constant. This acceleration of the rate of germination was followed by more rapid growth of the seedlings; particularly is this so when the shoots are considered; the plants from soaked seed were taller at 3 and 5 weeks and their leaves more fully expanded. It is, therefore, not surprising to find that the dry weight has also been increased by the treatment. As the plants then (5 weeks) bore well-formed buds in the series "soaked seed

for 24 hours at 24° C.," it is seen that the effects of the seed treatment have persisted far into the life-cycle of the plant. It was, of course, impossible to obtain root data from such a field trial, but the seed remains were, however, carefully removed, dried and weighed. Only 14 per cent. of the original dry weight remained so that, on making allowance for the testa, little food was left, at this stage the dry weight per 100 seeds was approximately equal for all the series; in the pot experiment when the seed remains were dug out with a considerable amount of the food left the difference in the rate of seed food utilisation was apparent. It is seen that soaking for 24 hours at 24° C. produced more effect than did soaking at a lower temperature, 14° C., or for a shorter period, 12 hours. The behaviour of the different weight-graded samples was similar, but the plants from small seed did not produce as much top growth as those from the heavier seeds.

Phaseolus vulgaris, *Dwarf Bean. Sutton's "Canadian Wonder."*

An autumn experiment was carried out with this species, the seed being soaked for 24 and 12 hours at 14° and 24° C. The plants were grown in a large unheated greenhouse in autumn, 1923.

From Table XXII it is seen that the early growth of the plants from soaked seed takes place more slowly than that of controls. The cold weather killed these plants, but had a differential effect, the controls resisted the adverse conditions better than seedlings from soaked seed.

Table XXII.

Effect of soaking Dwarf Bean Seeds.

Treatment	No. of visible hypocotyls, 14 days %	No. of visible hypocotyls, 17 days %	No. of plants alive, 25 days %
Control	58	87	49
Soaked 12 hours at 14° C.	38	66	21
Soaked 12 hours at 24° C.	59	77	29
Soaked 24 hours at 14° C.	47	71	25
Soaked 24 hours at 24° C.	29	51	18

Working with dwarf Beans, Kidd and West found that the temperature which brought out the effect of soaking varied for the different periods of soaking. They showed that despite an earlier start, the plants from soaked seed gave poorer growth. In the experiment here described soaking has produced slower growth and weaker plants.

A summer experiment with "Masterpiece" dwarf beans (Sutton's)

was carried out, ten replications of short rows of the soaked and control seed were sown. The growth of the seedlings was measured by height (to the centre of the bud) and by the size of the first leaves (length of mid rib and width at widest point) and finally by dry weight determinations made after six weeks' growth. The treated plants were compared replication for replication with the controls and the figures so obtained are averaged in column VII of Table XXIII.

Whilst plants from seed soaked for 12 hours at 14° and 24° C. appeared above the ground earlier, at three weeks the controls were taller and had larger leaves. A reduction of approximately 20 per cent. has been produced by soaking when the growth of the tops of plants from soaked and control seed is compared.

In both the experiments with this type of bean, it is seen that soaking the seed produces weaker and poorer seedlings, despite any acceleration of germination this treatment may cause; there is then no correlation between the rate of germination and the vigour of after-growth in the case of this species.

Table XXIII.

Dwarf Bean, "Masterpiece." Summer. Six weeks' growth.

I. Treatment	II. Percent. germin. 2 weeks. No. of visible shoots	III. Per-cent. estab-lished	IV. Height, 3 weeks, cm.	V. Length of mid rib 1st leaf, 3 weeks, cm.	VI. Width of leaf, cm.	VII. Dry wt. Total produce tops, gm.	VIII. Dry wt. of 100 tops in terms of control =100
Control	48	96	6·52 ± ·15 (100)	6·08 ± ·18 (100)	5·37 ± ·089 (100)	41·95 (100)	100
Soaked for 12 hrs. at 14° C.	61	86	4·58 ± ·19 (70·5)	3·99 ± ·18 (65)	3·01 ± ·14 (56)	29·80 (71)	73 ± 5
Soaked for 12 hrs. at 24° C.	51	93	5·64 ± ·18 (87)	4·87 ± ·21 (79)	3·78 ± ·15 (70)	35·20 (84)	77 ± 5·5
Soaked for 24 hrs. at 14° C.	61	97	4·98 ± ·13 (77)	4·78 ± ·14 (78)	3·65 ± ·16 (68)	38·34 (91)	77 ± 4
Soaked for 24 hrs. at 24° C.	36	84	5·33 ± ·16 (82)	4·42 ± ·24 (72)	3·82 ± ·16 (71)	32·3 (76)	81 ± 6·7

Dry wt. original seed per 100 = 43·4 gm.
Moisture content = 14·13 %.

Crimson Clover.

Seeds of a sample of "Early Red" Crimson Clover (Sutton's) were soaked in an excess of water for 24 and 12 hours at 14° and 24° C. The sample soaked for 24 hours at 24° C. sprouted during the treatment, a few seeds soaked for 24 hours at 14° C. also started to sprout, for this reason very great care to keep the seeds moist and uninjured whilst

sowing was exercised. The soil temperature was 12° C. when the seeds were covered. This transference into soil and covering may have accounted for the high mortality rate shown by those seeds soaked for 24 hours. The seeds were spaced in rows; after sowing, all the boxes were watered. Table XXIV shows the growth made from November 1st to February 1st.

The sample soaked for 24 hours at 24° C. gave poor total germination possibly due to injury caused by transference of sprouted seed during sowing, the sample soaked for 24 hours at 14° C., although it had begun to sprout gave a good total germination when compared to the control. This sample, however, showed a marked decrease in the yield, being 22 per cent. below the control. In the case of the higher soaking temperatures, a more marked decrease in yield is produced; this might possibly be caused by the shock of transference into soil at 12° C. Despite quicker initial germination, radicle emergence, growth has been retarded and a decreased yield was obtained by soaking the seed of this species.

Table XXIV.

Effect on Growth of Soaking Seed of Crimson Clover.

Sample	No. of visible shoots: Soil germin. 17 days %	No. of visible shoots: Total %	Average dry weight per 100, gm.	In terms of control =100
Control	40	59	·93 ± ·027	100
Soaked 12 hours at 14° C.	39	54	·91 ± ·026	97·8
Soaked 12 hours at 24° C.	25	53	·73 ± ·0255	78
Soaked 24 hours at 14° C.	38	53	·84 ± ·030	90
Soaked 24 hours at 24° C.	17	38	·68 ± ·034	73

Table XXV.

Growth after re-drying. Beans. Six weeks. Winter Growth.

Sample	Soil germin. 14 days %	Average height (cm.)	Average dry weight per 100, gm.	Average weight of 100 seed remains, gm.
Control	44	7·66 ± ·21	107·5	52·25
Soaked 12 hours at 14° C.	42	6·92 ± ·18	104·9	56·25
Soaked 12 hours at 24° C.	30	6·15 ± ·17	110·2	55·25
Soaked 24 hours at 14° C.	42	7·24 ± ·20	110·2	56·05
Soaked 24 hours at 24° C.	38	6·33 ± ·14	108·2	54·02

To test the effect of soaking and re-drying in air. Bean seeds that had been soaked for 12 hours and 24 hours at 14° and 24° C. respectively,

were spread out to dry on blotting paper in the air for four days. They were then stored in envelopes for 11 days and sown. These plants were removed from the pots in the greenhouse at the end of six weeks. They appeared equal in height.

From the above table it is seen that soaking and re-drying does not produce taller plants as did soaking—the controls here being the tallest—and does not cause the seeds to give up food more rapidly to the shoots as in the case of soaked plants. To produce the beneficial effect obtained by soaking, the seed must be sown at once.

VII. General Conclusions and Summary.

Experiments have been described which emphasise the importance of the condition of the seed at the time of sowing, because the condition of the seed affects not only the rate of germination, but also influences the subsequent growth of the seedling. With oats one of such conditions, the state of maturity, can be artificially altered by various drying methods which produce an increased vigour of germination and of subsequent growth. Careful husk removal favours an increased rate of germination and more rapid first leaf development and this effect can be traced throughout a long period in the life of the plant. Soaking the seed (oats) in water also increases the rate of germination and subsequent growth; from the germination tests of grain soaked in the presence of various oxidising agents, indications as to the vigour of subsequent growth were obtained.

Soaking the seed of several species of grasses—Cocksfoot, Timothy, Tall and Meadow Fescue and Rye Grass—also accelerated germination and stimulated growth to give higher yields of herbage. The results obtained with leguminous seeds varied as to species; whilst broad bean seeds soaked in water grow more rapidly, little effect was observed on peas, and a deleterious effect was produced by such treatments on dwarf beans and crimson clover, the cotyledons of which are epigeal.

There can be little doubt that a satisfactory start means a great deal to the growth and yield of such crops as oats. From the synopsis of experiments described (see Appendix) it appears that a definite correlation does exist between the vigour of germination and the rate of subsequent growth; in the case of oats, such a relationship has been demonstrated for rice by Kondo (15). By growing large numbers of samples it should be possible to estimate which daily count of germinated seeds[1]

[1] Or other index of rapidity = "energy."

The Effect of Soaking Bean Seeds upon Subsequent Growth.

Fig. 1. Seedlings three weeks old, controls (left) and seedlings from seed soaked for 12 hours at 24° C. × $\frac{1}{8}$th.

Fig. 2. Seedlings three weeks old from control (left) and seed soaked for 24 hours at 14° C. × $\frac{1}{8}$th.

Fig. 3. Seedlings from control (right) seed and seed soaked for 24 hours at 14° C., six weeks after sowing. × $\frac{1}{6}$th.

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in a standardised test gives the highest mathematical correlation with the subsequent growth.

That a similar correlation may exist in the case of several other Gramineae and also certain Leguminoseae is not at all improbable. There is then in such cases a possibility of devising tests by which further valuable information could be obtained from routine seed testing as to the capability of the tested sample to grow well under normal field conditions.

Work along these lines is being carried out.

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Appendix.

The author is indebted to Mr T. W. Fagan, M.A., F.I.C., Advisory Chemist, for the following figures showing an analysis of the garden soil used in all the soil experiments described.

Mechanical Composition.

	%		%
Fine gravel ...	13·8	Silt	13·2
Coarse sand ...	11·6	Fine silt	25·1
Fine sand ...	12·7	Clay	8·8

Chemical Analysis.

Moisture	4·02	Magnesium oxide (MgO) ...	0·49
Loss on ignition	11·66	Phosphoric acid (P_2O_5) total	0·23
Silica insoluble	72·75	,, ,, (,,) available	0·014
Iron oxide (Fe_2O_3)	5·84	Potash (K_2O) total	0·46
Alumina (Al_2O_3)	8·32	,, (,,) available ...	0·016
Calcium oxide (CaO)... ...	0·22	Nitrogen	0·36

The soil is a thin light loam, formed from the Aberystwyth grits, a sub-group of the lower Silurian. Compared with similar soils in the neighbourhood, it is better supplied with available phosphates, but like the large majority of these soils contains no carbonate of lime.

Synopsis of Experiments, showing the Relation between Vigour of Germination and Subsequent Growth.

Seed	Treatment	Effect on germination	Effect on growth	Correlation
Oats: Grey Winter	Hastening after ripening by drying	Increased rate of germination in sand and soil tests	Increased growth (7 winter weeks)	+
Rad. Sprig	Hastening after ripening by drying	Increased rate of germination in sand and soil tests		.
Ceirch du Bach	Careful husk removal	Increased rate of germination in sand and soil tests	Increased rate of 1st leaf development and rate of growth for six weeks (spring)	+
Grey Winter	Soaking in water	Increased rate of germination in sand and soil tests	Increased rate of growth. Six weeks (winter)	+
Black Bell III	Soaking in presence of excess carbon dioxide	Decreased rate of germination in sand tests	? Less increase than when soaked in tap water	? +
Wheat: Standard Red	Soaking in tap water	No difference in sand tests observed	Better growth than controls. Six weeks summer	? +
Standard Red	Soaking in presence of carbon dioxide	? No difference	Poorer than controls. Six weeks	? +
Cook's Wonder	Soaked in hydrogen peroxide (·56 Vol.)	Decreased rate of germination	Decreased growth	+
Cook's Wonder	Soaked in tap water	Increased 5th day figure germination	Increased growth rate	+
Cook's Wonder	Soaked in oxygen saturated solution	Increased rate of germination—3rd day figure germination	Increased growth at six weeks	+
Cook's Wonder	Soaked in 2 % $KMnO_4$ solution	Slightly slower germination	Increased growth rate. Six weeks	−
Per. Rye Grass	Soaking in water	Increased rate (energy) and total germination	Increased growth (five weeks summer)	+
Timothy				+
Full Leaved Fescue				+
Cocksfoot				+
Cocksfoot	Repeated experiments	Increased rate	Increased rate	+ again
Peas	Soaking for 12 hrs. at 14° C. and 24° C.	Increased energy figure (soil and sand)	? Increase top growth. Six weeks winter. (Results too near controls)	? +
Broad Beans	Soaking for 12 and 24 hrs. at 14° C. and 24° C.	Increased (soil and sand) rate of germination	More top growth (autumn, six weeks)	+
Broad Beans	Soaking for 12 and 24 hrs. at 14° C. and 24° C.	Increased (soil and sand) rate of germination	Summer, six weeks	+
Crimson Clover	Soaking 12 and 24 hrs. at 14° C. and 24° C.	Decrease rate of soil germination (? temp. effect)	Decreased rate of growth	+
Dwarf Bean	Soaking	Slower soil germination	Winter hardiness poor	? −
Dwarf Bean	Soaking	Increased rate of germination	Decreased growth. Summer	−

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BIOLOGICAL STUDIES OF *APHIS RUMICIS* LINN. FACTORS AFFECTING THE INFESTATION OF *VICIA FABA* WITH *APHIS RUMICIS*

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(With 5 Text-figures.)

CONTENTS.

I. Introduction.

The influence of the various factors which affect the infestation of plants by aphids has not received much investigation under controlled experimental conditions. Field observations, indicating that plants vary in their susceptibility to attack, due to such factors as soil conditions and climatic influences, have been recorded, and the influence of the varietal differences of plants on the liability to infestation has received some attention. While the accumulation of data from field observations is invaluable, especially if the data are collected over several seasons,

the number of factors involved makes a correct interpretation of them difficult and uncertain. Controlled experimental conditions may not faithfully represent the conditions obtaining in the field, but by the elimination of the complications due to varying factors, a more correct interpretation of the results is possible.

The experiments described in the present paper have been carried out with a view to investigating under controlled conditions, some of the factors which affect the infestation of *Vicia faba* by *Aphis rumicis*. The general principles involved and the results obtained have, however, a wider application to plant sucking insects in general.

A few papers which are of interest with respect to the results obtained in these experiments have appeared during the past few years.

Howard (9) discusses certain observations made in India on the influence of soil aeration, soil temperature and moisture on the growth of certain crops as affecting their susceptibility to insect attacks. The lowered vitality of the plant, owing to adverse conditions, is considered as predisposing the plants to heavier attacks.

Williams (15) discusses certain data regarding soil conditions and climate in relation to the outbreaks of the frog-hopper blight of sugar-cane (*Tomaspis saccharina* Dist.) in Trinidad.

Andrews (1) deals with the influence of soil factors and manurial treatment on the susceptibility of the tea plant to *Helopeltis theivora* Waterh. After careful consideration of data obtained from field observations and experiments, this author considers that local soil variation is one of the most important primary causes influencing the progress of the attack. Andrews found in the soils of three districts examined, that there is a correlation between the ratio of available potash to available phosphoric acid, the value of this ratio for a given percentage availability of phosphoric acid, and the soil acidity and the varying degree to which the tea gardens in the different districts suffer from the attacks of this insect. When soluble potash was supplied to the roots of tea bushes heavily infested with *Helopeltis*, the bushes threw off the attack entirely and remained free throughout the season. It would appear that by feeding the plant with substances specially suited for its growth, the plant juices have been rendered unsuited to the requirements of the insect.

The introduction of a toxic substance into the plant (usually trees) as a method of controlling an insect pest has been tried by some experimenters and a certain degree of success claimed for the method. Thus it has been claimed that the injection of barium chloride 1 : 350 into th

roots of apple trees infested with woolly aphis has resulted in the disappearance of the insect (14). Similarly potassium cyanide has been used against boring insects in forest trees. Considering the toxic nature of such substances and their possible effects on the plants, the application of this latter method is doubtless very limited.

The data given in the present paper, although they can only be considered as the results of a preliminary investigation of the subject, afford considerable evidence, that under different conditions of plant growth, the cell sap (which is the food of plant sucking insects) is affected, resulting in a greater or less infestation by aphids.

The following abbreviations are used in the text.

a.v. female	= apterous viviparous female.
w.v. female	= winged viviparous female.
c.s.d.	= calculated significant difference.
mean T.	= mean temperature.
2nd gen., etc.	= 2nd viviparous generation.

Thanks are due to Dr A. D. Imms for the many facilities he has kindly granted me for carrying out these experiments; to Dr W. E. Brenchley for advice regarding the growing of beans in pots and water culture; to Mr R. A. Fisher for assistance with the statistical considerations involved in the paper and to Mr J. Page for advice regarding some of the chemical aspects of the paper.

II. Technique and Methods.

The technique was devised so that the factors concerned should be the same for all comparable series in the experiments.

The Prolific Longpod variety of broad beans was used, it having been previously shown that this variety is highly susceptible to the attacks of *Aphis rumicis* (6). The bean seeds for all comparable series were planted on the same day, so that the age of the plants was the same.

In the soil series the plants were grown in ordinary 10-inch flower pots, one plant in each pot, the pots being coated on the outside with bees-wax in order to prevent excessive evaporation.

Unmanured soil from the laboratory farm was used, being screened and thoroughly mixed with 10 per cent. of Leighton Buzzard sand. Each pot held 18 lbs. of this mixture. The manurial substances shown in the various tables in section III were hand mixed with the soil for each pot. For the sand cultures, glazed Doulton porcelain pots were used, each pot holding 24 lbs. of Leighton Buzzard sand which was

washed with tap water. The chemical substances were added to the sand in each pot in the form of solutions.

The plants were kept in a large glass house specially designed with large windows and doors so as to allow free circulation of air (Fig. 1). They were kept covered with muslin bags so as to guard against outside infection. These covers cut out about 18 per cent. of light but this factor was the same for all the plants.

Fig. 1. Photograph of glasshouse showing the arrangement of the pots and the covers over the plants.

Pots 1 and 2 in left-hand row are covered with wire gauze cylinders. Pot 3 in the same row with a perforated zinc cylinder, the remainder of the plants are covered with muslin bags. The pots in right-hand rows are sand cultures.

Thermograph records of the temperature in the glasshouse were taken throughout all the experiments.

The same strain of *Aphis rumicis* was used throughout and winged migrants (from *Euonymus*) of the same generation was used as the basis of infection of the experimental plants each year. The history of the strain which was bred continuously from 1920 is briefly as follows. Two apterous viviparous females were taken from a wild colony on broad beans in May, 1920, and colonies produced from them were bred on Prolific Longpod beans. Female-producing sexuparae and males, which appeared in autumn, were transferred to small *Euonymus europaeus*

bushes and ova were eventually laid on them. In the spring of 1921 the ova hatched out and one fundatrix was isolated and became the stem mother of all the colonies used throughout the experiments. The agamic generations were reared on Prolific Longpod beans during the summer and arrangements were made so that when the oviparous females appeared in the autumn, they laid ova on *Euonymus*. Parthenogenetic generations were also carried on throughout each winter, by keeping the colonies on beans in a warm greenhouse. In this way fundatrices of the strain were available each spring, and at the same time, the strain was carried on in an unbroken series of agamic generations during the four years[1].

The aim of the experiments described in section III was to obtain a reliable figure for the number of aphids produced on Longpod beans in a definite time and to compare the numbers so obtained in different series, in which the plants were grown under different conditions. This is referred to as the "infestation figure" and the fixed period during which the aphids were reproducing on the plants as the "reproduction period." The infestation figure obtained on beans grown in unmanured soil is taken as the standard control figure, to which the infestation numbers obtained in the various series are referred. The infestation figure for one plant is obtained by infecting the plant with one a.v. female of a known generation and, at the end of a definite period, counting all the aphids present on the plant. The experiments were arranged in series and owing to the variation in the fertility of individual females, five plants have been used for individual counts in each series. Each plant was infected with one aphid and the mean of the counts for the five plants was taken as the mean infestation figure for the series concerned.

The reproduction period for comparable series occurred over the same days, so that the factors of temperature, sunshine and humidity were the same for all these series.

It was arranged that the reproduction period should be always in early summer, as previous observations indicated that the maximum reproduction occurs with the early parthenogenetic generations.

The methods employed in infecting the plants may be briefly described as follows.

One fundatrix of the pure strain was isolated on *Euonymus*. It produced a.v. females (occasionally one or two winged forms may be produced in the first generation). The second generation consists chiefly of

[1] A paper dealing with this aspect of the breeding experiments will be published shortly.

winged migrants. Two or three of these migrants were transferred to one "stock" bean plant for each of the different series. Each series, therefore, including the five plants reserved for obtaining the infestation counts, consisted of six plants. The object was to get at least five young aphids produced by the winged migrants on the stock plants of each of the series on the same day. The migrants produced a.v. females of the third generation and when about ten of these were produced on each stock plant, the winged parents were killed and the young aphids allowed to develop to maturity. The period from the time these young were born, until they reproduced, is referred to as the "developmental period." When these apterous females had passed the third moult and before they actually became adult, one female was transferred from the stock plant to each of the five plants of its respective series. The date and approximate time that each of the females began to reproduce on these plants was noted, and from that time onwards the colony was allowed to develop and reproduce freely for a definite period of time, usually 14 days. At the end of this reproduction period, the parts of the plants infested with the aphids were cut off and placed in bottles containing 70 per cent. alcohol, a separate bottle being used for each plant. The total number of aphids from each plant was counted and the mean infestation figure for each series taken as being the mean of the counts for the five plants in the series. The counts obtained for individual plants are not given in the tables for reasons of economy of space, but the mean infestation figure is given, together with the standard deviation calculated from the individual counts on the five plants in each series.

The actual dates on which the infections were made and the date of sowing the bean seeds in the various series are given in the text, in the remarks relating to the different tables.

It will be noted that the apterous females used to infect the plants in each series had been reared from birth to maturity on one of the plants of the series concerned. They were therefore under the food influence of the sap of a plant of their respective series. The length of the developmental period of these mothers varied a little. In favourable cases they all became mature on the same day. In some cases, however, especially where the plants of a series were under adverse conditions of treatment, the developmental period was more irregular and usually one or two days longer than in those series in which the treatment of the soil was more favourable to the plant.

It is seen therefore that the factors affecting the infestation figures were as far as possible the same for all comparable series, so that signi-

ficant differences between the mean infestation figures of different series can safely be attributed to the effect of the different manurial treatment or soil conditions.

The influence of the temperature during the reproduction period on the resulting infestation figures is well shown by comparing the figures for 1923 and 1924 and the necessity for having the reproduction period for all the series, which are to be compared, over the same period of days is evident. The mean T. of the reproduction period and the developmental period, referred to frequently in the text, has been obtained by calculating the mean T. for each day of the period from the maximum and minimum daily temperature in the glasshouse and taking the average of the mean T. of all the days in the period concerned. This is naturally only an approximation to the actual temperature throughout the period.

For the purposes of these experiments, any two series taken from any one of the tables in section III are considered as showing a significant difference in infestation, when the observed difference between the mean infestation figures for the two series is greater than twice the standard deviation calculated from the two mean infestation numbers of the series concerned.

III. Experimental Data.

The data obtained from the experiments are given in the tables I–VIII and the charts (Fig. 2, A–F) show the daily maximum and minimum temperature in the glasshouse during the reproduction periods. The following features of the experiments should be noted.

(1) The same strain of *Aphis rumicis* was used throughout the experiments.

(2) Apterous viviparous females of the same generation were used as the basis for infection each year.

(3) Prolific Longpod variety of broad beans was used throughout.

(4) The bean seeds in all the series of any one of the tables were sown on the same day.

(5) The reproduction period for the aphids on the plants in all the series of any one of the tables occurred during the same days.

The following table, which shows in detail the results obtained from a series of beans grown in unmanured soil during May, 1921, will explain the details associated with each series. The plants have been arranged in order of infestation figure.

The bean seeds were planted March 23rd, 1921. The stock plant was infected with two winged migrants (2nd gen.) from *Euonymus europaeus*

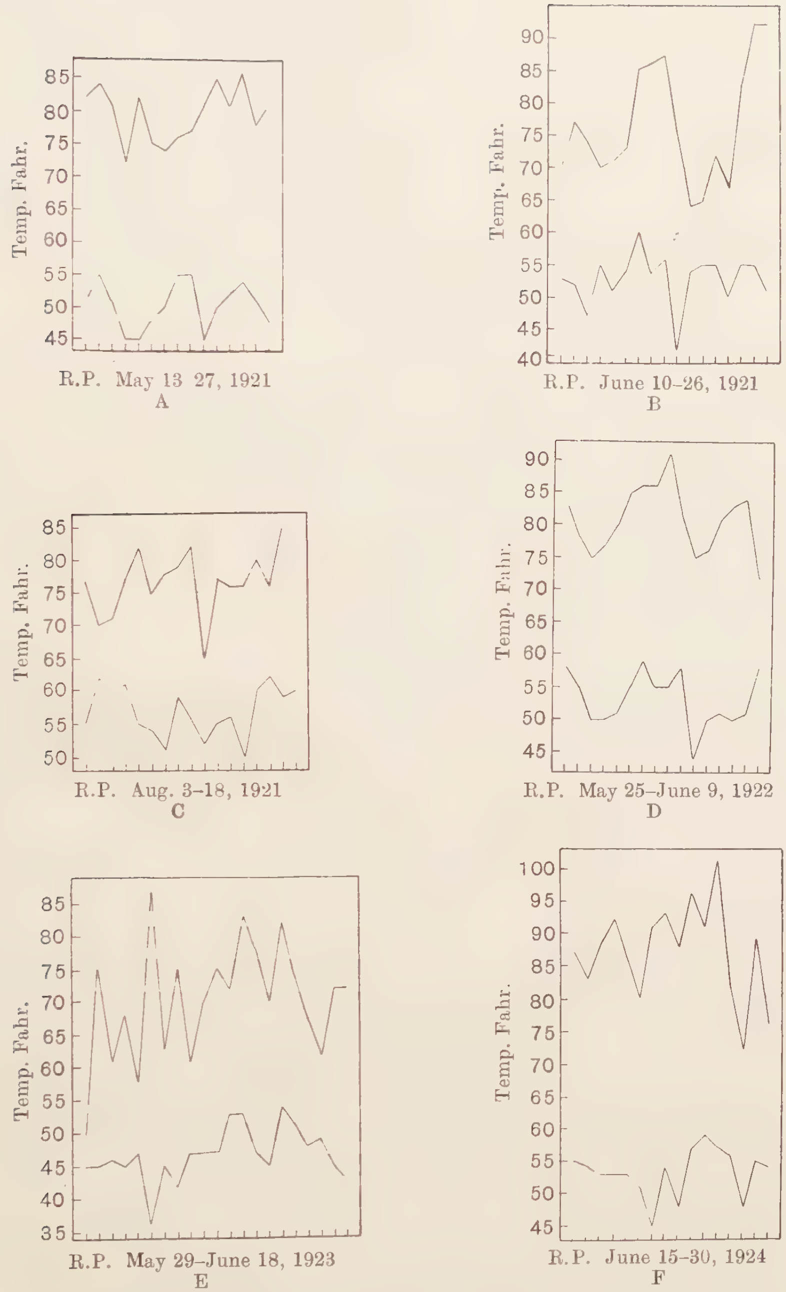

Fig. 2. Charts showing the daily maximum and minimum temperature in the glass-house during the reproduction periods R.P. in the various experiments.

Chart A refers to Table I, B to Table II, C to Table III, D to Table IV, E to Tables V and VI, F to Tables VII and VIII.

Table I. (1921.)

Reproduction period May 13th to 27th.

Plant No.	Treatment	Total aphids produced	Average per plant	Standard deviation
1	Soil unmanured	1205		
2	—	1147		
3	—	1015	1037	127
4	—	969		
5	—	848		
6	Stock plant	—		

on April 28th, 1921. They produced a.v. females, which reached maturity in 14 days, the mean T. during the developmental period being 58° F. Five of these apterous females were transferred to the five plants in the series, one female to each plant. Each one began to reproduce on May 13th, 1921, and after 14 days all the aphids produced on each plant were killed off and counted. The mean T. for the reproduction period was 64° F., with a record of 126 hours of sunshine.

The counts obtained on the plants are given in column 3 of the table. A few winged forms were present, the numbers on the different plants varying from 3 to 12, but on plant No. 3, 41 were counted. The number of winged forms present on the plants of the different series, as noted in the remarks on each of the following tables, includes only adult winged forms and well defined nymphs (3rd instar) of winged forms. There were doubtless some younger winged forms in the colonies which, owing to the wing pads not being developed, have not been diagnosed as such. The numbers given indicate a wide variation in winged production.

Under the conditions stated for Table I, therefore, a mean infestation figure of 1037 was obtained, with a standard deviation of 127.

The *A* series (Table II) consists of 11 groups, series A_1 being the control. The bean seeds were planted on May 8th, 1921. The stock plant of each series was infected with three w.v. females (4th gen.) on May 5th, 1921, obtained as follows. Winged migrants (2nd gen.) from *Euonymus* were transferred to Longpod beans and six a.v. females produced by them were isolated on a bean plant to form a colony. W.v. females (4th gen.) appeared about May 27th, 1921, and were used to infect the stock plants as noted above. From the a.v. females produced by these winged forms on the stock plant, one female was transferred to each of the five plants in the respective series. A 14-days reproduction period was given and the mean infestation figure obtained for each series is shown in column 3 of the table.

Table II. (1921.)

Reproduction period June 10–12th to 24–26th.

Series	Treatment (soil)	Total aphids produced (av. of 5 plants)	Standard deviation
A_1	Unmanured	728	95
A_2	1 gm. K_2SO_4 4 gm. superph. 1·5 gm. $NaNO_3$	867	112
A_3	1 gm. K_2SO_4	584 (Av. of 3 plants)	58
A_4	1·5 gm. $(NH_4)_2SO_4$	636	132
A_5	1 gm. $NaNO_3$	653 (Av. of 4 plants)	64
A_6	4 gm. superph. 1 gm. K_2SO_4	667	89
A_7	4 gm. superph.	796	92
A_8	5 gm. $MgSO_4$	580	86
A_9	0·75 gm. $MnSO_4$	787 (Av. of 3 plants)	209
A_{10}	0·4 gm. Na arsenite	655	228
A_{11}	0·75 gm. boric acid	534	—

The mean T. of the reproduction period was approximately 62° F. with 86–93 hours of sunshine. The apterous mothers used to infect the individual plants did not all come to maturity on the same day, so that the reproduction period on some plants commenced on June 10th and on others on June 11th or 12th. The developmental period of the apterous mothers varied from 10–12 days, the mean T. of the period being approximately 64° F.

It is seen that the mean infestation figure in series A_1 is lower than that obtained in Table I, the mean T. over the reproduction period being slightly lower and the aphids being of a later generation. Series A_2 treated with complete mineral manure shows an increase in infestation compared with A_1, the calculated significant difference (c.s.d.) being 132 and the observed difference 139. With the other series, owing to the low temperature which obtained throughout the experiment, and the resulting low infestation figures, there are no appreciable differences in the counts of the different series. The greater uniformity of the infestation figure in some of the series and the irregularity of the counts resulting in a high standard deviation in other series (*e.g.* A_9 and A_{10}) may be associated with the different manurial treatment of the plants, a factor which may also account for the irregularity of the developmental period of the apterous females in the different series. The winged forms present in series A_1–A_{11} were 29, 36, 3, 29, 4, 12, 17, 2, 19, 10, 2. It is

impossible to say whether this apparently wide variation in numbers is due to the varied treatment of the plants.

Table III. (1921.)

Reproduction period August 3rd–6th to 17th–20th.

Series	Treatment (soil)	Total aphids produced (av. of 3 plants)	Standard deviation
I	Unmanured, plants covered with muslin bags	649	58
II	Unmanured, plants covered with wire gauze cylinders	502	94
III	Unmanured, plants covered with perforated zinc cylinders	367	32

The series in Table III were arranged in order to test the effect of reduced light on the sap of the plants and the resulting influence on the infestation figures in the different series. Previous observations indicated that the carbohydrate content of the sap (sugars and starch) was an important factor affecting its feeding value for the aphids. With reduced light and photosynthetic activity, a decrease in the formation of carbohydrates would be expected. The plants in series I were covered with ordinary muslin bags which cut out about 18 per cent. of light. In series II, wire gauze cylinders were used which cut out about 35 per cent. of light and in series III, perforated zinc cylinders which cut out about 65 per cent. of light. The amount of light which passed through these covers was estimated with a thermopile. The bean seeds were sown on July 4th, 1921, the stock plant of each series being infected with two w.v. females (8th gen.) from beans on July 24th. The a.v. females transferred from the stock plants to the individual plants of the respective series began to reproduce on dates varying from August 3rd to 6th, the developmental period being from 9–12 days, those in series III having the longest developmental period. The mean T. of the developmental period was approximately 70° F. The increased developmental period in series III is evidently associated with the food factor. The reproduction period was 14 days with a mean T. of approximately 60° F.

These series were grown later in the summer than previous series and the aphids were of a later generation. The plants did not grow so well as earlier series. Nevertheless it is clear that series II and III give a lower infestation figure than the control series, which result is confirmed by repeat experiments. The decrease in infestation appears to be due to the reduced feeding value of the sap and not to the effect of the reduced light on the activity of the aphids.

The c.s.d. between series I and II is 128 with an observed difference of 147. Similarly the c.s.d. between series II and III is 114 with an observed difference of 135. A total of six winged forms were counted on the plants in series I, three in series II and none in series III.

Table IV. (1922.)

Reproduction period May 25th–26th to June 7th–8th.

Series	Treatment (soil)	Total aphids produced (av. of 5 plants)	Standard deviation
B_1	Unmanured	1417 (av. of 10 plants)	233
B_2	1·5 gm. K_2SO_4 5·0 gm. superph. 2·0 gm. $NaNO_3$	1587 (av. of 10 plants)	246
B_3	1·5 gm. $MgSO_4$	1474	353
B_4	1·5 gm. K_2SO_4	1503	241
B_5	1·0 gm. boric acid	1541	225
B_6	Unmanured, plants covered with wire gauze cylinders	1066	60
B_7	Unmanured, plants covered with perforated zinc cylinders	734	77

The *B* series (Table IV) consists of seven groups, series B_1 being the control. The bean seeds were planted on March 27th, 1922. The stock plant of each series was infected with winged migrants (2nd gen.) from *Euonymus* on May 15th, 1922. The plants in each series were infected each with one a.v. female from the respective stock plant on May 23rd, 1922. Some of these females began to reproduce on May 25th, others on May 26th, the developmental period being 8–9 days with a mean T. of 67° F. The reproduction period was 14 days with a mean T. of 67° F., and 160 hours of sunshine.

Series B_2 with complete mineral manures shows an increase in infestation numbers compared with B_1, but the observed difference of 170 is not significant, the c.s.d. being 215. The standard deviation of the various series is high, the individual counts being somewhat irregular. Series B_6 and B_7, which are a repetition of the series in Table III, confirm the results indicated in that table. The c.s.d. between B_1 and B_6 is 159 with an observed difference of 351 and between B_6 and B_7 is 98 with an observed difference of 340.

Tables V and VI consist of 11 series, the plants in the *C* series being grown in soil and those in the *D* series in sand. The bean seeds in all the series were planted on April 4th, 1923.

Table V. (1923.)

Reproduction period May 29th–31st to June 16th–18th.

Series	Treatment (soil)	Total aphids produced (av. of 5 plants)	Standard deviation
C_1	Unmanured (control series)	461	62
C_2	Watered with culture solution S (*vide* Table VI)	478	95
C_3	Unmanured, no sand added, soil packed tightly, heavily watered, badly aerated and waterlogged	483	117
C_4	Acid soil from Harpenden Common, unmanured (lime requirement 0·4)	476	165
C_5	Acid soil from Harpenden Common, treated with 2 oz. lime per pot	(av. of 4 plants) 475	87
C_6	Acid soil from Harpenden Common: 2 oz. lime, 1·5 gm. K_2SO_4, 4·0 gm. superph., 2·0 gm. $NaNO_3$	564	114

Table VI. (1923.)

Reproduction period May 29th–31st to June 16th–18th.

Series	Treatment (sand)	Total aphids produced (av. of 5 plants)	Standard deviation
D_1	Watered with culture solution S	483	151
D_2	Watered with culture solution S_1	677	132
D_3	Watered with culture solution S_2	1207	251
D_4	Watered with culture solution S_3	428	29
D_5	Watered with culture solution S_4	624	88

Owing to the failure of the ova laid on *Euonymus* the previous autumn, a colony of the same strain of *Aphis rumicis* which reproduced parthenogenetically throughout the winter was used for infection of the stock plants. Each stock plant of the various series was infected with two a.v. females on May 10th, 1923. They produced a.v. females and five of these were transferred from each stock plant, one female being placed on each of the five plants in the respective series. The apterous females began to reproduce on various dates from May 29th to 31st, the developmental period varying from 19 to 21 days. This long developmental period was due to the low temperature during the period, the mean being approximately 55° F. The period was, however, longer on some of the series than on others, evidently due to the food factor. A reproduction period of 18 days was given, the mean T. for this period being 58° F., with only 58 hours sunshine.

In series C_3 an attempt was made to create a badly aerated and waterlogged condition of the soil, but no appreciable difference in infestation has occurred (compare with C_1).

The acid soil used in the series C_4–C_6 was of poor quality, being light and sandy with a lime requirement of 0·4. The amount of lime added in series C_5 and C_6 was equal to twice the lime requirement.

The formulae of the culture solutions used in the D series are given below. The weights of the substances given in the formulae represent the amounts by weight which each pot in the appropriate series in Table VI received. Each solution was made up in concentrated form, six times the weights of the substances given in the formula being added to 2400 c.c. of distilled water. These concentrated solutions represented the total amount for the six plants of each appropriate series (five plants for the counts + the stock plant). After the seeds had germinated about 20 c.c. of the concentrated stock solution, diluted to 150–200 c.c. with ordinary tap water, was watered daily, or on alternate days, to each of the six plants in the series concerned. After about 20 days therefore each pot had received in solution the weights of the substances as indicated in the formula. In the series D_5, where the nitrogen was kept as low as possible, the dilution of the stock solution S_4 was made only with distilled water in order to avoid introducing nodule-forming bacteria.

Culture Solution S.

	gm.
KNO_3	2·0
$MgSO_4$	1·0
NaCl	1·0
$CaSO_4$	1·0
KH_2PO_4	1·0
Ferric chloride	0·04
Boric acid	0·02

This is a normal culture solution as used for water culture experiments, but the above formula represents double strength. Boric acid has been added, as recent work in the Botany Department at Rothamsted has shown that a trace of boron is necessary for the proper development of the bean plant.

Culture Solution S_1.

The formula is the same as that of solution S, except that NaCl has been replaced by 2 gm. of KCl, resulting in an increase of K in relation to phosphoric acid.

Culture Solution S_2.

The formula is the same as solution *S*, except that the $MgSO_4$ has been increased to 3 gm.

Culture Solution S_3.

	gm.
$(NH_4)_2SO_4$	1·2
$MgSO_4$	1·0
KCl	0·2
NaCl	0·5
$CaSO_4$	0·5
KH_2PO_4	0·3
Ferric chloride	0·04
Boric acid	0·02

This formula was devised with the aim of reducing potash and phosphates and at the same time relatively increasing the nitrogen. Previous observations indicated that the carbohydrates of the sap form the more important food for aphids.

Culture Solution S_4.

	gm.
KNO_3	0·7
KCl	1·0
NaCl	0·1
KH_2PO_4	0·5
$CaSO_4$	0·5
Ferric chloride	0·04
Boric acid	0·02

This formula was devised to give the opposite effect of solution S_3, the nitrogen being decreased relatively to the increase in K.

Owing to the effect of the low temperature on the development and reproduction of the aphids, the infestation figures of the *C* and *D* series are low. The addition of complete minerals in the series C_6 has resulted in a slight increase in infestation in that series, but the difference is not significant, the c.s.d. between C_4 and C_6 being 180 with an observed difference of 88. It is interesting to note that in the sand cultures there is a tendency to higher infestation figures than in the soil series, and this is more clearly shown in the 1924 experiments (Tables VII, VIII). Series D_3 shows a marked increase in infestation, the c.s.d. between D_1 and D_3 being 262 with an observed difference of 724, which is apparently due to the action of the increased $MgSO_4$. There is an increase in D_2 compared with D_1, the c.s.d. being 180, with an observed difference of 194 which appears to be due to the increase in potash. Series D_5, in which the K and phosphates are relatively increased in relation to the

nitrogen, shows a tendency to increased infestation compared with D_1, the c.s.d. being 156 with an observed difference of 141. Compared with D_4 the series D_5 gives an observed difference of 196 with a c.s.d. of 82.

A few winged forms were present on the different plants, the number in the series C_1–C_6 being 1, 2, 0, 8, 8, 4 and in D_1–D_5, 0, 6, 23, 4, 5. The increased production of winged forms in D_3 is probably associated with the higher infestation figures in this series and not due to a "wing producing" influence of the culture solution used.

Table VII. (1924.)

Reproduction period June 15th–16th to 29th–30th.

Series	Treatment (soil)	Total aphids produced (av. of 5 plants)	Standard deviation
E_1	Unmanured (control series)	1341 (av. of 4 plants)	174
E_2	K_2SO_4 2·0 gm. Superph. 6·0 ,, $NaNO_3$ 2·5 ,,	1923 (av. of 4 plants)	389
E_3	Watered with culture solution S (*vide* Table VI)	1340	291
E_4	KNO_3 4·0 gm. $MgSO_4$ 2·0 ,, $NaCl$ 2·0 ,, $CaSO_4$ 2·0 ,, KH_2PO_4 2·0 ,,	1944	235
E_5	KCl 3·0 ,, KNO_3 4·0 ,,	1375	287
E_6	$MgCl_2$ 3·0 ,,	1569	262
	KNO_3 4·0 ,,	1740 (av. of 4 plants)	238
E_7	Unmanured, bean plants six weeks older than E_1	548	262
E_8	Unmanured, plants covered with wire gauze cylinders	830	124
E_9	Unmanured, plants covered with perforated zinc cylinders	377	78

The bean seeds used in the E series (Table VI) were planted on April 27th, 1924, except E_7 (sown March 15th, 1924, the plants being six weeks older at the time of infection). The stock plant of each series was infected with two winged migrants (2nd gen.) from *Euonymus* on May 31st, 1924, and the a.v. females produced by them became adult about June 15th, having a developmental period of 12–13 days with a mean T. of 63° F. In the case of the series E_8 and E_9 however, the period was somewhat longer, varying from 14 to 16 days.

A reproduction period of 14 days was given, the mean T. being 71° F. with 130 hours of sunshine.

The weights of the chemical substances given in column 2 of the table show the quantity each pot received. In E_4 the substance present in culture solution S was hand mixed with the soil in the dry state, double strength being given. It was found that in soil treated with solution S the plants did not give such a high infestation figure as in the case of sand, but when the substances were added to the soil in the dry state an increased infestation figure was obtained (*vide* E_3 and E_4).

Owing to the comparatively high temperature obtaining during the reproduction period, the infestation figures are much higher than in the 1923 experiments (Tables V and VI). Series E_2 treated with complete minerals, compared with E_1, gives an observed difference of 582 with a c.s.d. of 420. Similarly, E_4 compared with E_1 gives an observed difference of 603, with a c.s.d. of 290. One plant in series E_1 and E_2 has been discarded as the infestation figures (352 and 504) for these plants were abnormally low, being obviously exceptional, due to the failure of the aphid colony (*vide* section IV, G). By replacing KCl in series E_6 with $MgCl_2$, an increased infestation figure compared with E_5 was obtained, which is interesting in respect of the result obtained in D_3 (Table VI). The c.s.d. between E_5 and E_6, based on five plants in the latter series is 358, with an observed difference of 194. One plant, however, in E_6 gave an abnormally low infestation figure of 886 and may be excluded. Taking the mean infestation figure of the remaining four plants in the series, the c.s.d. between E_5 and E_6 becomes 350, with an observed difference of 365. The reduced infestation figure obtained in E_7 shows the influence of the age of the plant. These plants were six weeks older than the control E_1 and were setting pods at the time of infection.

Table VIII. (1924.)

Reproduction period June 15th–16th to 29th–30th.

Series	Treatment (sand)	Total aphids produced (av. of 5 plants)	Standard deviation
F_1	Watered with tap water only	942	121
F_2	Watered with culture solution S	2125	268
F_3	Watered with culture solution S_1	2296	255
F_4	Watered with culture solution S_2	2266	694
		2463 (av. of 4 plants)	461
F_5	Watered with culture solution S_2 *a*	1995	444
		2139 (av. of 4 plants)	290
F_6	Watered with culture solution S_3 *a*	1665	414
		1870 (av. of 4 plants)	59

Series E_8 and E_9 are repetitions of previous series (Tables III and IV) and confirm the results previously obtained. The c.s.d. between E_1 and E_8 is 214, with an observed difference of 511, and between E_8 and E_9, 147 and 453 respectively.

The number of winged forms noted in the series E_1–E_9 were 0, 18, 0, 8, 0, 3, 6, 0, 0.

The F series consists of five groups, the dates of infection, sowing of seed, etc., being the same as for Table VII. The developmental period of the apterous mothers was 12–13 days, but in F_1 it averaged 14 days.

The formulae of the culture solutions S, S_1, S_2, S_3 and S_4 have been given on pages 485–6. Two new solutions are used in the F series. Solution $S_2\,a$ differs from S_2 in that NaCl has been omitted. In solution $S_3\,a$ potassium has been omitted, the formula being:

	gm.
$(NK_4)_2SO_4$	1·2
$MgSO_4$	1·0
NaCl	1·0
$CaSO_4$	1·0
NaH_2PO_4	1·0
Ferric chloride	0·04
Boric acid	0·02

The infestation figures are somewhat higher than in the soil series (Table VII). Untreated sand (F_1) gave a mean infestation figure of 942 as against 1341 on unmanured soil (E_1). In F_2 there is a marked increase in infestation compared with F_1 and E_1, and it is interesting that this increase does not obtain in E_3 compared with E_1 (Table VII). There is a tendency to increased infestation in F_3 compared with F_2, as was also observed in D_2 and D_1 (Table VI). An increase in infestation is indicated in F_4 compared with F_2 when one examines the counts on the individual plants in these two series. Owing, however, to the high range of variability in the counts in F_4 and the resulting high standard deviation, the observed difference is not significant. Two low infestation figures occurred in F_4, but as they do not deviate from the mean of the five plants in the series by more than twice the standard deviation, they are retained. The following are the counts on the individual plants in F_2, F_4 and F_5, the standard deviation in the two latter series being high.

Series F_2	Series F_4	Series F_5
2382	2803	2597
2336	2762	2350
2306	2614	1869
1857	1673	1841
1744	1480	1316

The observed difference between F_3 and F_6 is 426, with a c.s.d. of 234. One plant in F_6 gave an abnormally low infestation figure of 842 which was 1000 less than any of the other four plants, and deviated from the mean of the counts on the five plants by 823, the standard deviation being 414. This plant was therefore excluded and the mean calculated on the counts for the remaining four plants. Series F_6 shows a slightly reduced infestation compared with F_2, the observed difference being 255, with a c.s.d. of 230. When the mean infestation figure for F_6 is based on the five plants, an observed difference of 460 is obtained with a c.s.d. of 440. Owing to the high range of variability in the counts it is, however, doubtful if the differences are real.

The number of winged forms noted in the counts in the series F_1–F_6 were: 0, 17, 0, 0, 15, 36.

IV. General Conclusions and Discussion of the Results.

A. *General considerations.*

Aphis rumicis is a polyphagous aphid having a wide range of food plants. It has been shown (3, 5) that the degree of infestation of the different food plants varies considerably[1]. Since the food of aphids is the plant sap (7), one would expect that factors affecting the physiological condition of the host plant, thereby affecting the cell sap, would indirectly influence the metabolism of the aphids through the food factor.

The factors which affect plant growth may be classified under:

(*a*) Climatic factors, chiefly rainfall, daylight, temperature and sunshine.

(*b*) Soil factors, embracing the physical and chemical constitution

[1] Börner, 1921 (*Mitt. Biol. Reichanst. Dahlem*, Heft 21, pp. 195–200), considers that *Aphis papaveris* F. = *A. fabae* Scop. is the true bean aphis, and that *A. euonymi* = *A. rumicis* L. is distinct and does not infect beans. Börner distinguishes these two forms by the length of the hairs on the antennae and fore legs and by their food plants. The evidence put forward is too meagre to warrant the formation of two species. *A. rumicis*, as dealt with by the present writer, exhibits wide variation on different food plants. Further, experiments have shown that the summer generations of the bean aphis (*A. rumicis*) has a wide range of food plants in Britain and infects beans, docks, poppies, *Chenopodium*, etc., and is not restricted in its choice of food plants as Börner states to be the case in Germany. It might be noted that failure in an experiment to get an aphis to take immediately to a food plant, on which it is placed, is not necessarily proof that the particular plant is not one of its natural food plants. Börner, 1923 (*Rep. Intern. Confer. of Phytopathology and Econ. Entom. Holland*, p. 69), considers that, in my experiments with *A. rumicis* on different food plants (see references at end of this paper), I used a mixture of the two forms *A. euonymi* and *A. papaveris*. From the account given of my technique it will be seen however that the same strain of aphis was used throughout.

of the soil, its texture, aeration, temperature, moisture and acidity and the availability of food for the plant.

(*c*) Plant varieties in relation to (*a*) and (*b*).

The influence of factors such as temperature and humidity, acting directly on the aphids, have been considered in these experiments and since they were the same for all comparable series, it is evident from the results obtained, that the degree of infestation (measured by the number of aphids produced in a given time) is influenced by the manurial treatment of the plants. There is no evidence in favour of the generally accepted view, that weakly plants suffer heavier infestation than well-nourished ones. In fact well-nourished plants afford the best food for the aphids. Aphis infestation in the field occurs during limited periods, favourable temperature and weather conditions being necessary for the rapid progress of the infestation. One would expect therefore that well-nourished plants would more readily "out-grow" the checking influence of attacks than weaker ill-nourished plants. This, however, cannot be interpreted as meaning that weaker plants are more heavily infested.

It has been shown (5) that varieties of *Vicia faba* possess different degrees of susceptibility to *Aphis rumicis*, a feature which is also exhibited by varieties of apple stocks to *Eriosoma lanigerum* (12). It is also well known to be the case with vine stocks and *Phylloxera vastatrix*.

Staniland (12) has recently investigated the relation of the distribution of sclerenchyma in varieties of apple stocks to their resistance to *Eriosoma lanigerum*. The factor appears to be of some importance to the aphid, by affecting the accessibility of the plant tissues rich in sap. It does not, however, altogether account for the differences in susceptibility and anatomical differences do not explain the variation in susceptibility of different varieties of *Vicia faba*. The important factor is doubtless associated with the question of the suitability of the sap of the plant to satisfy the food requirements of the aphid. The digestion of the sap by these insects results from the action of the enzymes present in the saliva and in the digestive juices, which are secreted by the epithelial cells lining the gut. The saliva is able to convert starch into sugars (7, 4, 13) and digest the hemicelluloses of the middle lamella of the cell walls of the plant, which indicates the presence of diastase and probably cytase ferments. Very little is known, however, regarding the digestive processes in aphids, but one of the important factors which account for the association of aphids with particular food plants, appears to be the feeding value or suitability of the sap of different plants, for the species of aphids which live on them. A polyphagous species like *Aphis rumicis*

is evidently suited to live on a wide range of plants; nevertheless, as has been referred to above, it does not flourish equally well on all these plants.

The mechanism of suction and the means whereby the aphid abstracts its food from the plant host has been described in a previous paper (4). A somewhat schematic drawing of a longitudinal section through the head of *Aphis rumicis* is given in Fig. 3. The head is in the feeding position and the stylets are shown penetrating the tissues of a bean stem. The various structures associated with feeding will be understood by reference to the explanation of the lettering, but the reader should also refer to the detailed account (4).

The host plants are selected by the winged spring migrants and the winged forms of the summer generations, and the apterous offspring of

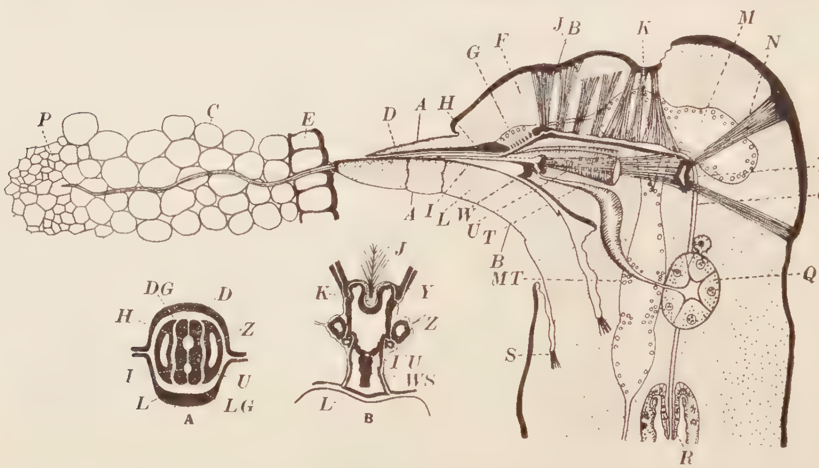

Fig. 3. Schematic longitudinal section through the head of *Aphis rumicis* × about 300 times, showing the insect in the act of feeding. The stylets are inserted into the tissues of a bean stem. Note the retracted labium (proboscis) and forward extension of the fore part of the head, which allows of the stylets being forced into the tissues to the maximum extent. When the stylets are withdrawn from the tissues, the fore part of the head is drawn back by the muscles *N* and the labium is pushed out to its normal length and the stylets then lie in the groove in the upper face of that structure. A, × about 1600 times, is a section through the head in the plane *AA* and B, × about 650 times, is a section in the plane *BB*.

C, cortex; *D*, labrum; *DG*, groove in labrum; *E*, epidermis; *F*, clypeus; *G*, gustatory organ; *H*, suction canal for plant sap; *I*, salivary canal; *J*, divaricator muscles of pharynx; *K*, pharynx; *L*, labium (proboscis); *LG*, labial groove in which the stylets lie; *M*, brain; *MT*, thoracic ganglion; *N*, retractor muscles of the fore-head; *O*, oesophagus; *P*, phloem; *Q*, salivary glands; *R*, valve to midgut; *S*, retractor muscles of labium; *T*, salivary duct; *U*, left maxillary stylet; *W*, salivary pump chamber; *WS*, stem of salivary pump chamber; *X*, pump muscle; *Y*, tentorium; *Z*, left mandibular stylet.

these winged females are dependent on the selection made. Doubtless one of the functions of the sensoria on the antennae of the winged forms is associated with the selection of suitable host plants, but by means of the gustatory organ (Fig. 3, G), the insect is able to appreciate the nature of the cell sap. This organ, which is present in all stages, is situated above the epipharynx, its sensory cells being in communication with the sap, as the latter passes along the pharyngeal duct, by means of pores in the epipharynx, as shown in Fig. 3[1]. The gustatory organ enables the insect to test the food before it enters the pharynx, the entrance of the plant juices into that structure being controlled by an efficient valve, which may be closed or opened at will, by the aphid, by means of powerful muscles (*vide* Fig. 3, B). In this way the insect is able to appreciate unfavourable food (sap) before it passes into the pharynx, and by keeping the valve closed, the passage of unsuitable food into the pharynx is prevented. The food, when drawn into that structure, is passed along the oesophagus to the mid gut, where digestion takes place. Regurgitation from the stomach is prevented by means of the oesophageal valve.

The following experiments and observations are of interest as showing the reaction of aphids to adverse food conditions.

Exp. 1. Two bean plants infested with a colony of *Aphis rumicis* were cut through, without disturbing the aphids, one plant being placed in a solution of $MgSO_4$ ($M/50$ strength = 2·4 gm. in 1000 c.c.) and the other in tap water. After about an hour the aphids on the former plant withdrew their stylets and wandered over the plant, while those on the latter remained undisturbed.

Exp. 2. Ten bean plants in soil (seeds sown July 20th, 1920) were each infected with one a.v. female. These females began to reproduce on August 15th, 1920, and after 11 days' reproduction the plants were removed, without disturbing the aphids, five being placed in bottles, each holding 500 c.c. distilled water and five in bottles containing 500 c.c. of $MgSO_4$ solution (strength $M/40$ = 3 gm. in 1000 c.c.). By August 29th many of the aphids in the latter series were wandering over the plants, while those in the former were undisturbed. The aphids were killed off and counted on September 2nd, 1920, the mean infestation figure for the $MgSO_4$ series being 590, that for the water series 780. The mean T. of the reproduction period was 62° F.

Cut stems of bean plants infected with aphids were also placed in dilute aqueous solutions of eosin and safranine. The stains could be

[1] *Vide* Davidson (4). The structure of the gustatory organ has been investigated by the writer and the paper will shortly be ready for publication.

watched as they were drawn up the plant. Soon after the solution arrived at an area of the plant where the aphids were feeding, they became restless, withdrew their stylets and wandered away, and after about two hours practically all the aphids on the plants were actively wandering.

Similar observations were made on plants growing in water culture. On those plants grown in normal culture solution, the aphids were usually collected in a close colony on the upper part of the stem. On the plants grown in solutions having no potassium, the aphids were not so numerous and leaving the growing tip of the plant they distributed themselves over the stem and beneath the leaves, as though they found the sap not suitable to their requirements. *Aphis rumicis* reared on dwarf French beans and Laxtonian peas, developed into quite small individuals, as was also the case when they were reared on older branches of *Euonymus* (6). On well-nourished bean plants the aphids grow bigger than on poorly nourished plants. Beans grown in unmanured soil do, however, afford satisfactory food for the aphids. Even when grown in sand the plant makes fair progress owing to the large seeds. The dry weights and nitrogen content of 1000 aphids taken from (*a*) unmanured bean plants and 1000 from (*b*) plants treated with complete minerals were estimated, the figures being as follows:

	Av. dry weight in gm. per aphid	Nitrogen in dry matter %	Nitrogen gm. per aphid
(*a*)	0·215	7·04	0·0157
(*b*)	0·258	7·18	0·0182

The manuring of the plant appears to have had a definite effect in increasing the dry weight of the insects and therefore the absolute nitrogen content, but it is doubtful whether the difference in per cent. nitrogen in dry matter of the aphids from manured and unmanured plants is significant.

There is no doubt, from the above observations, that aphids react to changes in the sap of the host plant. One is therefore led to the view that the significant differences in infestation described in section III are due to variations in the feeding value of the sap of the plants, associated with the increase of young growth, these variations being chiefly due to the different treatment of the soil. The problem from the point of view of economic entomology is, whether changes can be induced in the sap of the growing plant, so as to affect its suitability as food for the aphids, and at the same time not adversely affect the plant. Differences in the degree of susceptibility, with different

varieties of the same plant, may be due to genetic factors, and this appears to be well worth consideration by the plant breeder.

B. *Influence of Temperature and Humidity.*

The influence of temperature on infestation is well shown by comparing the figures for 1923 (Tables V and VI) with those for 1924 (Tables VII and VIII), the mean T. for the reproduction period being 58° and 71° F. respectively. In the former series the temperature during the reproduction period of 432 hours was below 58° F. for 270 hours and above 71° F. for only 35 hours, while in the latter series, with a reproduction period of 336 hours, it was below 58° F. only for 88 hours and above 71° F. for 124 hours.

In 1923, unmanured soil (C_1) gave a mean infestation figure of 461, whereas in 1924 E_1 gave 1341. In order that the infestation figures may be examined more closely, we must consider the influence of temperature on the developmental period of the aphids and on the number of young produced daily by individual females. There is little data of this kind, based on controlled temperature conditions, available, chiefly due to the difficulty of controlling temperature over a long period in a glass-house. A comparison of data obtained with reference to the mean T. of the developmental period is however valuable; in fact data of this kind about aphids are almost worthless unless temperature is taken into account.

(a) *Influence of temperature on the developmental period.*

The effect of temperature on the length of the developmental period of the agamic females is one of the most important factors affecting the infestation figures. With an increase in temperature, up to the optimum, the length of the developmental period is reduced, and it follows that, for a definite reproduction period, the resulting infestation figures (other factors being the same) will be greater the higher the temperature. Headlee (8), working with *Toxoptera graminum* under constant temperature conditions, has shown that increase in temperature produces a decrease in the developmental period. Baker and Turner (2), with reference to the mean T. of the developmental period, obtained the same result with the apple-grain aphis (*Rhopalosiphum prunifoliae* (Fitch)). Lathrop (10) has investigated this question more fully with *Aphis pomi* D.G. The developmental periods for a number of agamic females were obtained and compared with the mean temperatures for the periods. When these data were plotted, temperature against time (developmental

period on days), the points obtained were found to lie approximately on a hyperbolic curve, having a formula which may be expressed as follows:

$$\text{Developmental period in days} = \frac{180}{\text{Temp. in degrees Fahrenheit} - 41}.$$

It was found that 41° F. was the critical temperature for this species, below which development practically ceased. By subtracting from the developmental period, the time during which the temperature was below 41° F. (non-effective temperature), the duration of the effective temperature was determined and a more accurate indication of the actual developmental period obtained.

Data regarding the developmental period with reference to the mean T. obtained for *Aphis rumicis*, when reared on Prolific Longpod beans grown in unmanured soil, are given in Table IX.

Table IX.

Year	Date of birth of a.v. female	Developmental period in days (av. of 5 aphids)	Mean T. of developmental period, ° Fahr.
1913	18. viii.	12	62
1920	16. vi.	8	71
1920	12. vii.	9	68
1921	28. iv.	14	58
1921	28. v.	11	65
1921	24. vii.	9	70
1922	16. v.	9	67
1923	10. v.	20	55
1924	3. vi.	13	63

In Fig. 4 a calculated curve is given, the points on which have been derived from Lathrop's formula $180/T - 41$. The data given in columns 3 and 4 of the above table have been plotted with reference to this curve. It is seen that the points so obtained approximate to a curve of the Lathrop type. This is also the case with the data obtained by Headlee for *Toxoptera graminum* under constant temperature conditions. It will, of course, be understood that the critical temperature may not be the same for all species of aphids.

(b) *Influence of temperature on the daily production of young.*

Headlee (8), working with *Toxoptera graminum* under constant temperature conditions, has shown that increase in temperature results in an increase of the number of young produced daily by the agamic females. Sanderson (11) has also shown this to be the case from data obtained by Hunter. There are no definite data on this point available

from the experiments with *Aphis rumicis*, but observations made throughout the experiments show that it does obtain in this species. An indication of the average daily production of young with this species is shown in Table X. The data were obtained from a number of a.v. females (offspring of wild w.v. females), which were isolated on broad beans on August 18th, 1913. The details of eight of these apterous females are given; three others which produced a few aphids and died after a few days have not been included as they were evidently exceptional. It should be noted that the aphids were of a late summer generation.

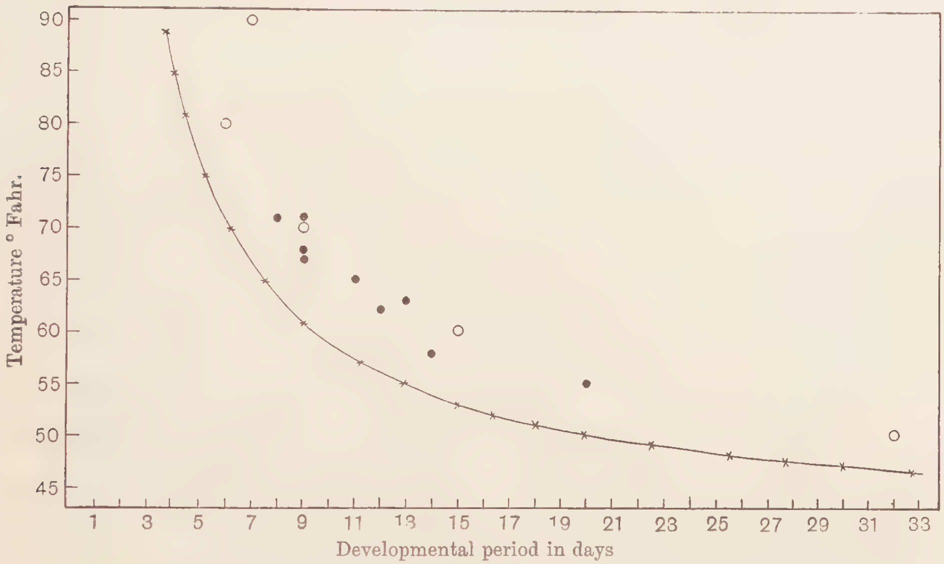

Fig. 4. Calculated curve showing the developmental period for *A. pomi* D.G. at different mean temperatures. The points are calculated according to Lathrop's formula $180/T - 41°$. The points ○ are from data obtained by Headlee for *Toxoptera graminum* and the points ● are from data obtained in the present experiments with *Aphis rumicis*. See further explanation in the text.

(c) *Influence of temperature on infestation.*

We can now examine the infestation figures of the various series given in section III with reference to the mean T. of the reproduction period, and the effect of this temperature on the developmental period of the aphids and the daily production of young. From data of this kind it is possible to calculate approximately the number of aphids expected on any day of the reproduction period. In Fig. 5 two calculated reproduction curves are given, showing the reproduction rate for *Aphis rumicis* on unmanured Longpod beans under the conditions of

Table X.

Aphid No.	Total young produced by a.v. female	Av. daily production of young	Developmental period of first-born in days	Mean T. of developmental period
1	41 (11 days)	3·7	12	
2	42 (12 „)	3·5	13	
3	26 (10 „)	2·6	14	
4	20 (10 „)	2·0	11	62° F.
5	35 (10 „)	3·5	10	
6	37 (9 „)	4·1	10	
7	45 (11 „)	4·1	11	
8	37 (10 „)	3·7	11	
Mean	35 (10·4 days)	3·4	11·5	

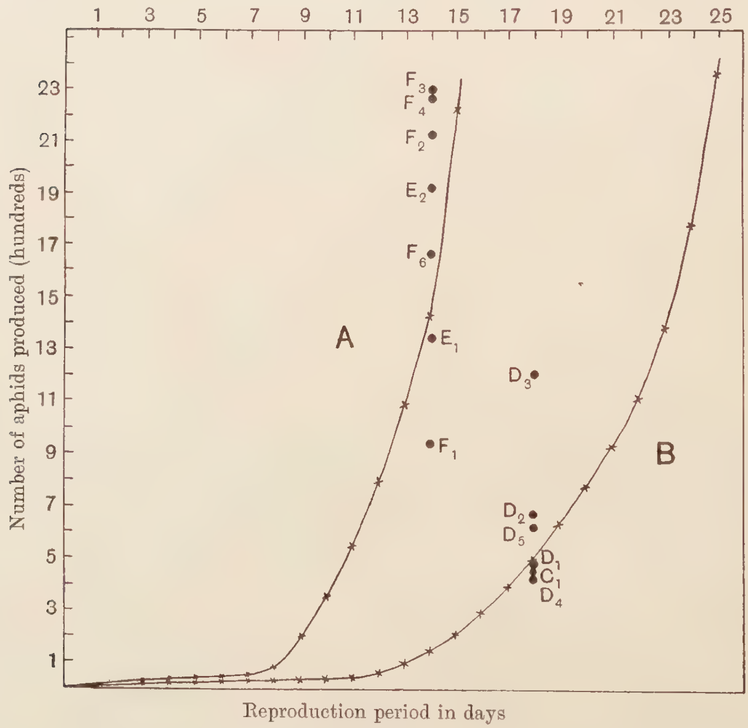

Fig. 5. Calculated curves showing reproduction rate of *Aphis rumicis* under different temperature conditions. The points marked × show the calculated number of aphids expected at the end of each day of the reproduction period, commencing with one adult a.v. female. For curve *A* the mean T. of the reproduction period was 71° F. For curve *B* the mean T. was 58° F. The points ● represent observed counts in the experiments. See further explanation in the text.

temperature obtaining in 1923 (series C_1) and 1924 (series E_1) respectively. The points on the curves have been calculated from data based on the remarks made in the previous paragraphs. The data for the 1923 curve (B) have been taken as follows:

(1) Mean T. of reproduction period, 58° F.

(2) Developmental period of the aphids, 11 days.

(3) Average daily production of young by the agamic females, 4.

(4) Average total number of young produced by one female, 52.

For calculating the 1924 curve (A), the data used were: (1) 71° F., (2) seven days, (3) seven young, (4) 56 young.

The data used in calculating the A curve were selected as giving, for a calculated 14 days' reproduction, the nearest fit to the mean infestation figure obtained in series E_1 (1924), and in the case of the B curve, the nearest fit for an 18 days' reproduction to the mean infestation figure in series C_1 (1923). The number of adults and the total number of aphids produced were taken into account in fitting the calculated numbers to the observed counts, so that the curves represent a fair approximation to the reproduction rate under the conditions stated. In the B curve, the calculated number of aphids expected at the end of the eighteenth day is 29 adults and 501 total aphids, the observed mean infestation count for series C_1 being 26 adults and 461 total aphids. In the A curve the calculated number of aphids at the end of the fourteenth day is 1429, the observed mean infestation figure for series E_1 being 1341. The points on the two curves were obtained by calculating the total number of aphids expected at the end of each 24 hours for each curve, and plotting these numbers against time. The position of the mean infestation figures obtained in certain series of the 1924 experiments (E and F series) are shown with reference to the calculated number for 14 days' reproduction on the A curve, and similarly those for certain series of the 1923 experiments (C and D series) are shown with reference to the calculated number for 18 days' reproduction on the B curve. It would clearly afford a valuable check on the observed infestation figures, if in experiments of this kind, the necessary data were obtained, so that curves showing the expected reproduction rate could be calculated.

The influence of temperature is seen at a glance by comparing the infestation figure for the same day in both curves. Thus on the fourteenth day on the A curve, the calculated number of aphids is 1429, whereas on the B curve it is only 149.

Temperature is an important factor affecting the degree of infestation in the field. During the summer of 1924 the temperature generally was

unfavourable for rapid increase of aphids, and there have been few outbreaks of *Aphis rumicis* in the south of England. Many fundatrices which hatched out on *Euonymus* in the open, on warm days at the end of April, were killed off before they reached maturity, owing to the low temperature and bad weather conditions obtaining afterwards. This failure of the formation of early colonies greatly affected the subsequent distribution of the species. The weather conditions obtaining in early spring, when the young colonies of aphids are being established and also in autumn when the winged sexuparae are migrating to the winter hosts is an important factor affecting the prevalence of aphids in the following season.

The relationship between the optimum temperature for the growth of the host plant and that for the development and reproduction of the aphids is an important consideration with reference to the infestation of cultivated plants by these insects. With plants growing normally at temperatures which are not sufficiently high to allow of the rapid increase of the aphid colonies, the progress of the infestation would be slow and the young shoots of the plants would not suffer serious damage. Similarly the relationship between the optimum temperature for the rapid progress of aphis infestation and that for the development of the parasites and predaceous enemies of aphids, is probably an important consideration. These biological aspects of the infestation of plants by aphids are worthy of further investigation.

(d) *Influence of humidity on the aphids.*

Definite experimental observations on humidity in relation to the temperature have not been made in these experiments. Generally speaking, a wide range of humidity does not produce any marked effect on the metabolism of these insects, as was shown by Headlee (8) to be the case with *Toxoptera graminum.* A fair degree of humidity was always maintained in the glasshouse during the experiments, the house being regularly sprayed inside with water, and during hot days the roof and sides outside were sprayed twice a day. Humidity records of the atmosphere in the glasshouse were taken during the earlier experiments, the humidity ranging from about 40 degrees at the mid-day period to about 90–100 during the few hours after midnight. With moderately high temperatures, dry atmospheric conditions are fatal to *Aphis rumicis*, as the writer has experienced when colonies have been reared in a heated glasshouse.

C. Influence of manurial treatment and soil conditions on infestation.

The differences in infestation counts obtained in the various series have already been noted in section III and it is only necessary here to briefly discuss those cases in which significant differences have been obtained. In those series where the soil was treated with complete mineral manures an increased infestation, compared with unmanured soil series, occurred in every case. With series A_1 and A_2 the difference is just significant, with B_1 and B_2 almost significant and with E_1 and E_2 markedly significant. In E_1 and E_4 the increase due to the liberal manurial treatment is strikingly shown and similarly in the sand cultures there is a marked increase in F_2 compared with F_1.

From the results obtained with sand cultures (Tables VI and VIII) the relative increase in potash and phosphates appear to have affected the feeding value of the sap, resulting in increased infestation. Series D_2, treated with solution containing increased potassium in relation to phosphoric acid, shows a significant increase compared with D_1. Similarly D_5 shows an increase over D_1. In series D_4 the potassium and phosphates are decreased in relation to nitrogen, resulting in a significantly lower figure than in D_5, in which the K and phosphates have been relatively increased. Series F_6, in which the solution used had a low K content, shows a significant reduction in infestation compared with F_1, as is also the case when compared with series F_3, in which the solution used had a higher K content. Potash makes for increased sugars in the plant and it may be that the increased infestation is associated with the increase in carbohydrates. (See also remarks on the influence of light on infestation, p. 502.)

The marked increase in infestation in D_3 is interesting as being apparently due to the increased $MgSO_4$ in the solution used. The plants in this series grew larger than any of the other D series and had a rich green colour and a big root development. In F_4 the increase in infestation over the control series F_2 is small, but the individual counts of the five plants in the former series indicate a tendency to higher infestation. Owing to the high temperature during the reproduction period the reproduction of the aphids in the control series was already high, so that one would not expect such a marked increase as occurred in the series D_3.

It is interesting to note that with the plants grown in sand cultures the infestation figures are higher than on those grown in soil (compare E_3 and F_2). This may be due to better aeration of the roots or to the increased growth of young juicy tissue, resulting in the sap being

more readily available for the aphids. It is possible that the soil reacted on the solution and somewhat changed its composition, because when the constituents of the same culture solution were added to the soil in the dry state (E_4), there was a distinct increase in infestation.

Acid soil (Table V) did not appreciably affect the infestation, although when lime and complete minerals were added there was a slight increase. Similarly, tightly packed, water logged soil conditions (C_3) did not affect the infestation. The results of the 1923 series are however not conclusive, owing to the low temperature and the resulting low infestation figures obtained.

The results obtained afford evidence that the infestation of plants by aphids is influenced by the soil conditions in which the plants are grown and by its manurial treatment and an investigation of this question from the plant physiology and biochemical standpoint is desirable.

D. *Influence of Light on infestation.*

The chief value of daylight for the plant is due to the part it plays in the rôle of photosynthesis. By reduction of the light available for the plant, the efficiency of these processes is interfered with and presumably the quality of the cell sap is affected. The results given in Tables III, IV (B_6 and B_7) and VII (E_8 and E_9) show clearly that, by reducing the amount of light available for the plants, the infestation is also reduced. The plants, under reduced light conditions, grew somewhat spindly and etiolated, having a small leaf area. They were however quite succulent and it would seem that the decrease in infestation is due to a reduced carbohydrate content of the sap.

Some results which were obtained in winter, by growing beans under artificial light, are interesting in this respect. The experiments were designed with the object of investigating the effect of light and temperature on the development of sexual forms in *Aphis rumicis* and are not strictly comparable with the present experiments. The data given in Table XI are however comparable, in that the reproduction period of the aphids in the illuminated and non-illuminated series was during the same days and under the same temperature conditions. The plants were of the same age and grown in the same soil.

P. L. beans were grown in a heated glasshouse, series *B* receiving the ordinary hours of daylight and series *A* in addition 7 hours of artificial light daily. The artificial light was obtained by means of two 500 c.p. tungsten filament lamps, the *B* series being shut off from the *A* series

Table XI.

No. of exp.	Reproduction period	Total aphids produced: A. Illuminated series	B. Non-illuminated series	Mean T. ° Fahr. of reproduction period
1	22. xi. 22 to 6. xii. 22	110	30	68
2	6. xii. 22 to 20. xii. 22	76	61	70
3	20. xii. 22 to 3. i. 23	106	43	67
Heating of glasshouse stopped on 3. i. 23; illumination stopped on 15. i. 23				
4	3. i. 23 to 24. i. 23	51	—	
	3. i. 23 to 31. i. 23	—	35	

by a black screen[1]. There were only two plants in each series, each plant being infected with two a.v. females. The total number of aphids produced in 14 days is given and it is seen that the figures are higher in series A than in B in each case. The infestation figures are low, but the time of the year is unsuitable both for the plants and for the agamic reproduction of the aphids.

E. *Influence of age of plants on infestation.*

It is a well known observation that aphids generally favour young growing shoots and the effect on *Aphis rumicis* when reared on older branches of *Euonymus*, compared with young shoots, has been already described (5). Aphids invariably migrate to the young growing parts of the plant, which evidently afford the best food conditions. The practice of cutting off the growing tips of young bean plants in this way reduces the chances of infestation. The infestation in series E_7, in which the plants were six weeks older than the controls (E_1), is considerably less than on the younger plants, the mean in the former case being 548 and 1341 in the latter.

This indicates a change in the feeding value of the sap as the plants grow older, and the value of early sowing where possible, so that the beans may be well advanced before the aphids are about, is evident.

F. *Influence of different varieties of* Vicia faba *on infestation.*

The infestation on different varieties of *Vicia faba* has been fully dealt with in a previous paper (6).

[1] A paper dealing with these experiments will be published shortly.

G. *Variability of the infestation figures on individual plants in the series.*

The variability of the infestation counts on the individual plants is important in relation to the true value of the mean infestation figure obtained from five plants[1]. With an increase in infestation figures there is a tendency to greater variability in the counts for individual plants, thus three unmanured series gave an average standard deviation of 167, whereas three comparable series, treated with complete minerals, gave an average standard deviation of 249.

Certain features associated with the aphid, the plant and the technique, may be considered as factors affecting the individual variation.

It is seen from the data in Table X that the length of the developmental period, the daily production of young and the total number of young produced, varies with individual females. The effect of this on the variability of the final infestation counts for a given reproduction period is evident.

Occasionally an exceptionally low count is obtained for one plant in a series, as is seen in A_5, E_6 and F_6. This is evidently due to the abnormally low fertility of the original female and the individual cannot therefore be considered as a normal representative of the colony. The infestation figures for the individual plants in the three series referred to above are given below.

Table XII.

Series	Infestation counts	Mean	Standard deviation
A_5	761		
	653		
	630	653	132
	590	(av. of 4 plants)	
	74		
E_6	2068	1740	238
	1835	(av. of 4 plants)	
	1632		
	1425	1569	262
	886	(av. of 5 plants)	
F_6	1929	1870	59
	1924	(av. of 4 plants)	
	1825		
	1803	1665	414
	832	(av. of 5 plants)	

[1] *Vide* Davidson, J. (1922). *Ann. App. Biol.* IX, 125–45, Statistical Appendix by R. A. Fisher.

It is evident that the count of 74 in series A_5 is exceptional and if included in calculating the mean, a fair average would not be obtained. With the other two series, however, the case is not so clear. The low counts of 886 and 832 deviate from the mean of the five counts in their respective series by more than twice the standard deviation. As these low counts would therefore only occur occasionally in a series of trials, they have been rejected and the mean of the four remaining counts taken.

It has been shown that the fertility of the aphids is affected by the varying nutrition of the plant, individuals on poorly nourished plants being less fertile than those on well nourished ones. This is, of course, a factor of importance when comparing the infestation figures in the different series. It is, however, possible, seeing that plants grown under the same conditions exhibit considerable variation in size and dry weights, that differences in individual plants may to some extent affect the individual infestation figures. It is difficult to ensure uniform conditions for the plants within a series of pot cultures. Such factors as soil moisture, soil temperature and the uniform distribution of the manures in the soil, are variants which may react on the plant, thereby affecting the individual aphid counts within a series. Variable local temperature conditions in the glasshouse may be of importance with reference to the position of the pots in the house. In these experiments the plants in each series were kept together for convenience, but it would be better if the pots were distributed throughout the house at random, in order to overcome the possible effect of localised temperature conditions.

One important point of the technique is the necessity for noting the actual time the original apterous female commences to reproduce on each plant, so as to definitely fix the exact time the reproduction period begins. Similarly, the aphids on each plant should be killed off exactly at the end of the allotted reproduction period. Naturally with about 100 plants under observation this is not actually practicable and the reproduction period on some plants may be many hours more or less than the exact period. The effect of this on the variability of the individual counts is not great when moderate temperature conditions obtain, but it is important when the progress of the infestation is rapid owing to high temperatures, as will be readily understood by reference to the curves in Fig. 5. In the A curve, eight hours more or less than the actual 14-day period, would result in an increase or decrease of about 300 aphids from the calculated figure. In order to minimise the liability to high variation in the individual counts, and to allow of significant differences appearing, it follows that a comparatively short reproduction

period must be allotted if the temperature during the reproduction period is high. The high counts in the F series, for instance, are subject to a high degree of error.

V. Summary.

(1) A technique has been developed, whereby the influence of various factors such as temperature, manurial treatment, soil conditions, age and variety of the plant on the infestation of beans by *Aphis rumicis* can be tested.

(2) Factors which influence the physiological activity of the plant, thereby affecting growth and the nature of the cell sap, affect also, through the food factor, the progress of the aphis infestation.

(3) Experiments have been carried out during four years, the methods employed being fully described. The chief features of the technique are: (*a*) The same strain of aphis was used throughout and infestations were made with sisters of the same generation for all comparable series. (*b*) The same variety of beans was used throughout and with comparable series the plants were always of the same age. (*c*) The reproduction period in all comparable series extended approximately over the same days, so that temperature and other climatic factors were the same for all the series.

(4) The experiments were in series, each series consisting of five plants, each plant being infected with one a.v. female. The aphids present on each plant at the end of a definite reproduction period were counted and the mean of the counts for the five plants was taken as the mean infestation figure for the series concerned.

(5) Temperature influences the developmental period of the aphids and also the daily production of young, thereby affecting the infestation figures, so that the reproduction period for all comparable series was taken during the same days.

(6) Significant differences in infestation have been obtained with certain series, these differences being considered as indicating differences in the feeding value of the plants in the different series.

(7) Beans grown in soil treated with complete mineral manures became slightly more heavily infested than those grown in unmanured soil. In unmanured sand low infestation figures were obtained.

(8) Beans grown in sand watered with normal culture solution gave higher infestation figures than those grown in soil watered with the same solution.

(9) Beans supplied with increased potash indicated increased infestation figures, whereas with low potash a decrease was obtained.

(10) Beans grown in sand watered with culture solution containing increased $MgSO_4$ showed a marked increase in infestation.

(11) Experiments repeated for three years, in which varying amounts of daylight were available for the plants, show that with reduction of the light, a decrease in infestation is obtained. Similarly in winter when artificial light, in excess of the ordinary daylight, was used, an increase in infestation was obtained compared with those plants which only received daylight. This is probably associated with the carbohydrate content of the plant sap and the decrease in young growth.

(12) Bean plants six weeks older than the controls gave a marked decrease in infestation figures.

(13) Beans grown in acid soil and in badly aerated soil conditions, did not show any difference in infestation, compared with the control series, but owing to the low temperature during the reproduction period the results are inconclusive.

(14) The relation between the optimum temperature for the growth of the host plant and that for the development and reproduction of the aphids is an important consideration with reference to outbreaks of aphis infestation.

(15) The results obtained in these experiments show that aphids react to physiological changes in the host plant. They problems have a wide application to plant-sucking insects in general, but the experiments only represent a preliminary investigation of a wide and important subject.

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STUDIES ON *OSCINELLA FRIT* LINN.

SUPPLEMENTARY DATA ON THE RELATION BETWEEN VARIETAL DIFFERENCES OF OAT PLANTS AND SUSCEPTIBILITY TO INFESTATION

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CONTENTS.

I. Introductory Remarks.

The important fact that varietal differences among oats may influence the extent of infestation of stem and grain by the frit-fly having been demonstrated (3), the extension of this line of investigation, to determine (1) whether such observed differences in extent of infestation among varieties would be maintained under the different climatic conditions of another year and (2) how far the constancy of such differences would be influenced by age of shoot, was clearly indicated. Provided these differences are proved to be of economic value and maintained by the oat varieties, it will then be necessary to investigate the factors limiting infestation in certain varieties, in order that the plant breeder may be provided with some of the essential basic facts before attempting to produce a resistant variety.

In this publication are recorded the results of a second variety trial, conducted during the year 1924 and following a similar trial in 1923,

with the aim of deciding these two questions and for this purpose attention was concentrated on the two least and the two most severely attacked varieties, as determined by experiment during the previous year (3). Otherwise experimental procedure and method of analysis were identical in the two years and, to avoid unnecessary recapitulation, the reader is referred to the above paper for descriptions of sites, length and spacing of drills, weight of seed sown and methods of observation, sampling and analysis of data.

The four varieties of oat selected were *Goldfinder* and *New Abundance*, which had previously given the best yields of frit-free grain, and *Superb* and *Supreme*, which had the worst records. In addition to these, three other varieties, namely *Waverley*, *Bountiful* and *Tartar King*, were included as they constitute the varieties of Messrs Gartons' spring oats on the market which had not previously been examined. Drills of *Goldfinder*, *New Abundance*, *Supreme* and *Superb* were sown on April 1st and again on April 23rd in the two localities, Sandford-on-Thames, Oxon., and Harpenden, Herts. The remaining varieties, *Waverley*, *Bountiful* and *Tartar King*, were included in the second sowing only. The oats sown on April 1st showed above ground on April 21st (later sowing, May 4th) and stem sampling was carried out on June 13th.

Our thanks are due to Mr Buckhurst, who undertook the analysis of the oat stems, at Harpenden.

II. EXPERIMENTAL DATA.

The scale of the experiment is clearly indicated by the minimum, mean and maximum number of plants and stems in the samples (which numbered six or seven for each variety) taken on June 13th, which were (*a*) at Oxford, earlier sown drills, *plants*, 88, 122, 151, and *stems*, 217, 281, 338; later sown drills, *plants*, 102, 132, 154, and *stems*, 397, 538, 693: (*b*) at Harpenden, early sown drills, *plants*, 38, 64, 80, and *stems*, 83, 146, 206; later sown drills, *plants*, 78, 99, 113, and *stems*, 247, 309, 344 respectively.

The arithmetic mean percentage infestations of stem and grain for the varieties of oats under observation, together with the standard errors of the means are shown in the order of sowing in Table I. With the exception of the variety *Superb* (first sowing) the percentage infestations of the stems were remarkably similar in the two localities.

The effect of a difference of even two weeks, in the times of appearance above ground of the plants of the two sowings, was most marked with the varieties *Goldfinder* and *New Abundance*, the first sowings of

Table I.

Arithmetic mean percentage of infestation with standard error.

O = Oxford. H = Harpenden.

E = above ground April 21st; remainder above ground May 4th.

Name of Variety		Stem (omitting shoots 0–3 ins. in length)	Grain
Goldfinder (E)	O	36·1 ± 5·2	4·3 ± 0·61
	H	37·3 ± 4·7	5·8 ± 0·29
New Abundance (E)	O	48·7 ± 5·2	5·7 ± 0·85
	H	42·2 ± 6·3	5·1 ± 0·83
Supreme (E)	O	55·1 ± 4·0	5·3 ± 0·58
	H	53·5 ± 5·1	5·9 ± 0·26
Superb (E)	O	52·0 ± 3·8	7·9 ± 1·07
	H	41·1 ± 7·3	7·7 ± 1·42
Goldfinder	O	62·3 ± 2·2	21·6 ± 1·26
	H	61·8 ± 2·2	22·8 ± 0·66
New Abundance	O	62·7 ± 1·6	25·4 ± 2·05
	H	56·0 ± 2·5	15·1 ± 0·98
Supreme	O	63·1 ± 2·3	22·2 ± 1·66
	H	64·6 ± 2·6	15·7 ± 0·95
Superb	O	66·4 ± 2·6	20·5 ± 0·65
	H	61·2 ± 2·7	10·5 ± 0·65
Waverley	O	69·9 ± 2·9	24·3 ± 1·09
	H	58·5 ± 5·8	13·7 ± 0·83
Bountiful	O	66·7 ± 3·1	22·3 ± 1·68
	H	63·2 ± 3·4	13·8 ± 1·17
Tartar King	O	68·7 ± 2·0	23·0 ± 1·00
	H	64·2 ± 3·4	11·5 ± 1·09

which suffered least stem infestation. With the second sowing infestation was very even throughout.

The grain infestation also indicated that the time factor operated with considerable effect. The grain of the first sowing suffered a negligible infestation (5 per cent.), while that of the second sowing was infested to the extent of 10–20 per cent. Considerable variation occurred at Harpenden with the second sowing, but very even figures were obtained at Oxford.

III. Statistical Analysis of Data.

(a) *Coefficients of correlation.*

The coefficients of correlation, together with their probable errors, which have been calculated from the experimental data, are recorded in Table II.

These coefficients of correlation are admittedly based on short series, but they serve to bring out very forcibly the effect of even two weeks' difference in the times of appearance of the first stems above ground, which was very marked in each locality.

Table II.

A. *Stem.*

(*a*) Arithmetic mean percentage infestation, Oxford:	
1. With Harpenden, first sowings	$+0{\cdot}77 \pm 0{\cdot}13$
2. With Harpenden, second sowings	$+0{\cdot}08 \pm 0{\cdot}25$
3. First sowing, 1924, with 1923 results	$+0{\cdot}79 \pm 0{\cdot}13$
4. Second sowing, 1924, with 1923 results	$+0{\cdot}79 \pm 0{\cdot}12$
5. First with second sowings, 1924	$+0{\cdot}48 \pm 0{\cdot}26$
6. First sowing with tillering capacity	$+0{\cdot}85 \pm 0{\cdot}09$
7. Second sowing with tillering capacity	$+0{\cdot}55 \pm 0{\cdot}18$
(*b*) Arithmetic mean percentage infestation, Harpenden:	
8. First sowing, 1924, with 1923 results	$+0{\cdot}76 \pm 0{\cdot}14$
9. Second sowing, 1924, with 1923 results	$+0{\cdot}64 \pm 0{\cdot}20$
10. First with second sowings, 1924	$+0{\cdot}49 \pm 0{\cdot}25$

B. *Grain.*

1. First sowings, Oxford with Harpenden	$+0{\cdot}79 \pm 0{\cdot}13$
2. Second sowings, Oxford with Harpenden	$-0{\cdot}03 \pm 0{\cdot}25$
3. Stem with grain infestations:	
First sowing, Oxford	$+0{\cdot}59 \pm 0{\cdot}22$
First sowing, Harpenden	$-0{\cdot}12 \pm 0{\cdot}29$
Second sowing, Oxford	$+0{\cdot}09 \pm 0{\cdot}20$
Second sowing, Harpenden	$-0{\cdot}03 \pm 0{\cdot}28$

Correlation between the Oxford and Harpenden stem infestations of the first sowing was as decided as that obtained in 1923, and in each locality a decided correlation was found to exist between these results and those obtained in 1923. In neither locality were the stem infestations shown by the plants of the first and second sowings at all definitely correlated. The younger plants of all varieties were equally lacking in powers of resistance to attack.

As in the previous year, there was no evidence of correlation between the stem and grain infestations either at Oxford or at Harpenden. With the first sowing the grain infestations at Harpenden and Oxford were decidedly correlated, but with the second sowing there was no correlation whatever.

(b) *Varietal differences in extent of infestation.*

The data recorded in Table I have been subjected to statistical analysis (1) to determine the significance of observed differences in infestation and (2) to combine the evidence available from the independent experiments, in exactly the same manner as has been previously described (3).

The results of such analysis for both stem and grain infestations are shown in Tables III and V respectively, and the evidence obtained from

the work of the two seasons 1923 and 1924 has been combined in Tables IV and VI.

Stem Infestation, Tables III and IV. Among the first sown varieties *New Abundance* again proved to be in no way inferior to *Goldfinder*, while *Superb* was in a doubtful position. In 1923 this variety compared with *Goldfinder* was more heavily infested to the extent of 17·2 per cent., but in 1924 in neither locality were the observed differences significant. Thus the difference of 14·7 per cent. indicated in Table V, though it is a summation of the observed facts, leaves us in a position of great uncertainty as to the comparative susceptibility of this variety. *Supreme* maintained its position as the most heavily infested variety, the results from the two seasons being almost identical, the final result being that the weighted mean difference in percentage infestation was 17·3.

Considering now the later sown varieties, it will be seen by reference to the tables that none of the observed differences were of high value and that none were significant. Thus, the inference appears to be that

Table III.

Stem Analysis.

O = Oxford. H = Harpenden. E = First sowing.

Variety		Difference between arithmetic mean percentage infestations (D)	Standard error of $D = Exy$	$\frac{D}{Exy}$	Weighted mean difference in percentage infestation (X)	Standard error (E) of X	$\frac{X}{E}$
Supreme (E)	O	19·0	6·5	2·83	17·4	4·7	3·68
	H	16·2	6·9	2·33			
Superb (E)	O	15·9	6·4	2·49	11·9	5·2	2·28
	H	3·8	8·7	0·44			
New Abundance (E)	O	12·6	7·3	1·72	9·0	5·3	1·68
	H	4·9	7·9	0·62			
Goldfinder (E)	Variety with minimum arithmetic mean percentage infestation with which the above have been compared						
Supreme	O	0·8	3·1	0·26	1·7	2·3	0·7
	H	2·8	3·4	0·82			
Superb	O	4·1	3·4	1·19	1·8	2·4	0·7
	H	−0·6	3·5	0·17			
New Abundance	O	0·4	2·7	0·15	−2·1	2·1	1·0
	H	−5·8	3·3	1·76			
Waverley	O	7·6	3·7	2·06	4·7	3·2	1·5
	H	−3·3	6·2	0·53			
Bountiful	O	4·4	3·8	1·15	3·0	2·8	1·1
	H	1·4	4·1	0·34			
Tartar King	O	6·4	3·0	2·13	5·0	2·4	2·1
	H	2·4	4·1	0·59			
Goldfinder	Variety with which the later-sown varieties have been compared						

Table IV.

Stem.

E = First sowing.

Variety		Weighted mean difference in percentage infestation	Standard error of difference	Weighted mean difference in percentage infestation for the two seasons (X)	Standard error (E) of X	$\frac{X}{E}$
Supreme (E)	1924	17·4	4·7	17·3	3·00	5·77
	1923	17·2	3·9			
Superb (E)	1924	11·9	5·2	14·7	3·59	4·09
	1923	17·2	5·0			
New Abundance (E)	1924	9·0	5·3	5·4	3·73	1·45
	1923	1·9	5·3			
Goldfinder	Variety with minimum infestation, with which the others have been compared					

Table V.

Grain Analysis.

O = Oxford. H = Harpenden. E = First sowing.

Variety		Difference between arithmetic mean percentage infestations (D)	Standard error of $D = Exy$	$\frac{D}{Exy}$	Weighted mean difference in percentage infestation (X)	Standard error (E) of X	$\frac{X}{E}$
Superb (E)	O	3·6	1·23	2·92	2·87	0·93	3·08
	H	1·9	1·45	1·31			
Supreme (E)	O	1·0	0·84	1·18	0·26	0·35	0·74
	H	0·1	0·39	0·03			
New Abundance (E)	O	1·4	1·07	1·31	0·16	0·67	0·24
	H	−0·7	0·88	0·08			
Goldfinder (E)	Variety with minimum arithmetic mean percentage infestation with which the above have been compared						
Goldfinder	O	1·1	1·42	0·78	9·00	0·78	11·60
	H	12·3	0·93	13·30			
New Abundance	O	4·9	2·15	2·28	4·63	1·03	4·50
	H	4·6	1·18	3·90			
Supreme	O	1·7	1·78	0·96	4·17	0·96	4·34
	H	5·2	1·15	4·52			
Waverley	O	3·8	1·27	3·00	3·45	0·81	4·26
	H	3·2	1·06	3·02			
Bountiful	O	1·8	1·81	1·00	2·76	1·07	2·58
	H	3·3	1·34	2·92			
Tartar King	O	2·5	1·19	2·10	1·80	0·87	2·07
	H	1·0	1·27	0·79			
Superb	Variety with which the later-sown varieties have been compared						

Table VI.

Grain.

Variety		Weighted mean difference in percentage infestation	Standard error of difference	Weighted mean difference in percentage infestation for the two seasons (X)	Standard error (E) of X	$\frac{X}{E}$
Goldfinder	1924	9·0	0·78	4·4	0·59	7·52
	1923	1·3	0·97			
New Abundance	1924	4·6	1·03	7·0	0·78	8·93
	1923	10·3	1·48			
Supreme	1924	4·2	0·96	2·9	0·65	4·40
	1923	2·5	1·04			
Superb	Variety with the minimum infestation, with which the others have been compared					

time is of the utmost importance in enabling the plant to reach a resistant stage, thereby confirming observations on this subject made in the following paper (4), and further, that varietal differences only become effective in relation to immunity after the plants have become established. Varietal differences were therefore of no value to the plant in the young stage during the years in question, and these data, in conjunction with the observation that immunity to infestation is pronounced after the fourth leaf stage has been passed (4), suggest that resistance is dependent on a physical factor, such as resistance of cuticle, which may prevent the newly-hatched larva from gaining entrance to the stem. This possibility is now being investigated.

Grain Infestation, Tables V and VI. No marked differences were observed with either the first or second sowings, except in the one case of the variety *Goldfinder*, at Harpenden, where the second sowing of this variety was comparatively heavily infested.

The evidence from the two seasons' work indicates that small varietal differences in resistance to attack do occur, but that constant values for these differences are unlikely to occur over a period of years, because extent of infestation of the grain is so largely dependent on the history of the crop during the growing period.

IV. Summary.

During the year 1924 additional data, in relation to varietal resistance to attack, were collected by repeating as nearly as possible the investigation conducted during the previous year, with the exception that only

those varieties of oat were used, which were most (*Goldfinder* and *New Abundance*) and least resistant (*Superb* and *Supreme*).

During the second season, during which, on the whole, conditions were unfavourable to damage by frit fly, varietal differences were again effective so far as stem infestation was concerned. The two varieties, *Goldfinder* and *New Abundance*, were significantly resistant as compared with the variety *Supreme*, similar differences being observed in the two seasons. Very late sowing indicated that varietal differences among very young plants were ineffective in influencing extent of infestation.

Small significant differences were observed in relation to the grain infestation, but from the evidence available it would appear that constant values for these differences are unlikely to occur over a period of years, because extent of infestation is largely dependent on the history of the crop during the early growing period.

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STUDIES ON *OSCINELLA FRIT* LINN. THE CORRELATION BETWEEN STAGE OF GROWTH OF STEM AND SUSCEPTIBILITY TO INFESTATION

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(With 3 Charts, 1 Graph and 1 Text-figure.)

Introductory Remarks and General Experimental Procedure.

It is believed that the most likely solution of the practical problem of controlling Frit Fly is to be found in the discovery or breeding of oat varieties comparatively resistant to attack. Such a variety may quite possibly be evolved by chance in the course of the work on oat hybridisation which is being carried on in many places, but if it should not, then it seems necessary for the plant breeder to attempt deliberately to build up a resistant oat, and for this purpose he must be provided with information as to the characteristics which are either responsible for, or coincident with, resistance to Frit attack. In this connection it is a matter of general observation that oat crops which have reached a certain stage of growth in the spring by the time the flies have appeared are less damaged than those which are younger, and the same observation holds in the case of the second brood attack on the grain. Further, Cunliffe (2) has suggested that the maximum prevalence periods of the fly in the field are fairly constant in time from season to season. On this assumption a solution of the problem would be obtained if the breeder could evolve a spring oat in which the rate of growth were so adjusted that coincidences between the most susceptible stages and the periods of maximum prevalence of the fly did not occur.

However, as far as we are aware, except for one indecisive experiment[1], no attempts have been made to ascertain the exact limits of growth between which susceptibility to attack is most pronounced. During the last year or two certain data bearing on this subject have been collected, both independently and in collaboration at Harpenden and Oxford, and in the interests of other workers on the subject should perhaps be placed on record although they are not as precise as is desirable. The whole series of experiments is an extension of, and complementary to, the work by Fryer and Collin (3) on the susceptibility of the oat grain to infestation by Frit Fly.

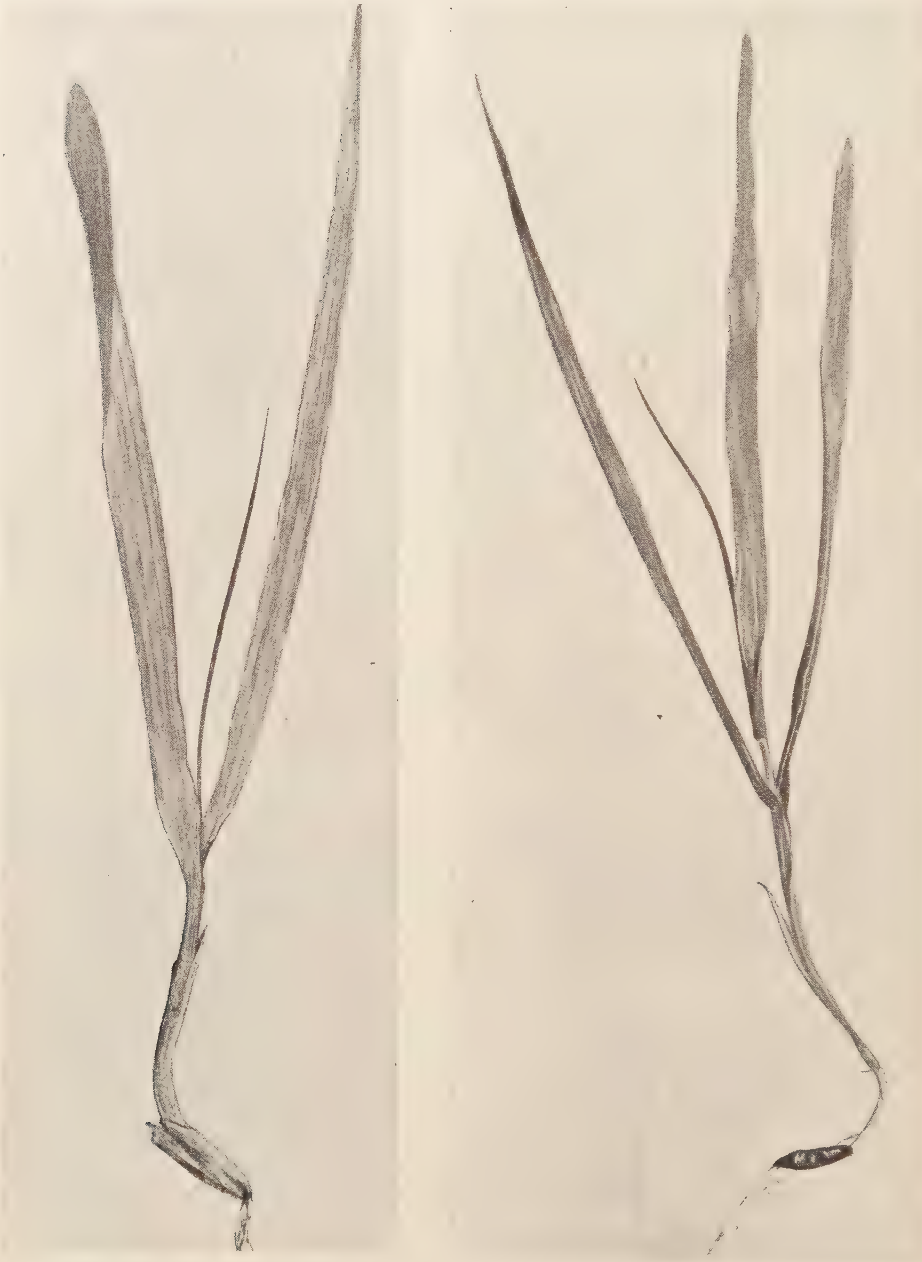
At Harpenden the experiments were conducted in the garden of the Pathological Laboratory, and at Oxford on the University Farm, Sandford-on-Thames, Oxon., by the courtesy of Prof. Somerville.

As a preliminary to investigating the susceptibility to attack of the young plant in its various stages of growth it is clear that some means of recording these stages must be adopted and, up to the present, it has been found that the most reliable criterion is extent of leaf formation, which is dependent on the factors of environment (soil and climate) and time.

During growth the oat stem passes from the one-leaf stage to the seven-leaf[2] stage, and then produces its panicle externally. The change from any one leaf-stage to the next, *i.e.* the formative period of a new leaf, may be arbitrarily divided for descriptive purposes into three stages, namely (1) *early stage*, when the new central leaf is just appearing, this condition being denoted in the following charts as "E"; (2) *medium or typical stage*, when the central leaf is half-grown, *i.e.* is very obvious but not more than half the length of the leaf previously formed, denoted as "M" (*vide* Fig. 1); and (3) *late stage*, when the length of the central leaf equals or exceeds that of the previously formed leaf, denoted as "L." For example, a plant in the three-leaf medium stage is described on the charts as "3 M." The main stems of any population of oat plants may thus be readily assigned to typical stages of growth within their respective leaf-classes for identification purposes. As some guide to the rate of growth it may be mentioned that during May the formative period of each leaf is approximately seven days in the case of oats sown in April.

[1] This experiment indicated that a fall in susceptibility might be expected early in the growth period of the stem, but gave no hint, except by measurement, of the limits of growth as related to susceptibility.

[2] The total number of leaves produced before the extrusion of the panicle seems to vary; some plants gave a total of eight leaves, and the number produced may be dependent on environmental conditions.



(*a*) Medium three-leaf stage (3 M) (*b*) Medium four-leaf stage (4 M)

Fig. 1. An oat plant in the medium or typical four-leaf stage (*vide* p. 517)

Whether or no rate of growth—as opposed to stage of growth—is a factor affecting susceptibility is as yet undetermined.

The principle underlying all the experiments was to expose oat plants of known history to the attack of the Frit Fly at different periods of growth, screening them from the fly before and after exposure. At the commencement and termination of each exposure period typical examples of the plant population were preserved for reference purposes. In every case only the first or main stem was considered in estimating infestation because young plants with infested main stems were necessarily forced to tiller[1]. An adequate period was always allowed for larval development so that the extent of the infestation could be observed with the assistance of a binocular microscope. Control plants, not exposed throughout their periods of growth, showed no infestation and proved that the screening was effective.

Experiment I. Harpenden, 1923. *Chart* 1.

Seven series of sowings of *Abundance* seed, at the rate of ten seeds per pot, were made in pots on March 15th and at the following intervals —namely, 14, 28, 42, 56, 63, and 70 (May 24th) days thereafter. The plants were grown in a fly-proof insectary, constructed of wire gauze. Exposures to fly attack in the field were made from each series of plants weekly, for seven day periods, from April 16th to June 11th inclusive. The actual numbers of plants exposed at one time from any one series averaged 14, the minimum and maximum numbers being 9 and 16 respectively. While in the cage the oats suffered considerably from the fungus *Erysiphe graminis* and also from the direct effects of lack of light and a humid atmosphere, but the latter were not so great as had been anticipated.

The variations in extent of infestation per cent., together with the limits of leaf development during the exposure period for each series of plants, are shown in Chart 1, plotted against dates of sowing.

The very limited number of plants would tend to emphasise the result of casual oviposition and a chance error in diagnosis[2] would unduly influence the observations, therefore a broad view of these results must be taken. No attack was observed until the exposure period May 22–28 and then apparently very few flies were at work as infestation was negligible, even of plants in the three-leaf stage. Certain series were heavily infested during the next two exposures, the attack falling off again during the last exposure.

[1] *Vide* footnote, p. 525.

[2] The presence of a *Tarsonemus* species of mite in some cases rendered diagnosis difficult.

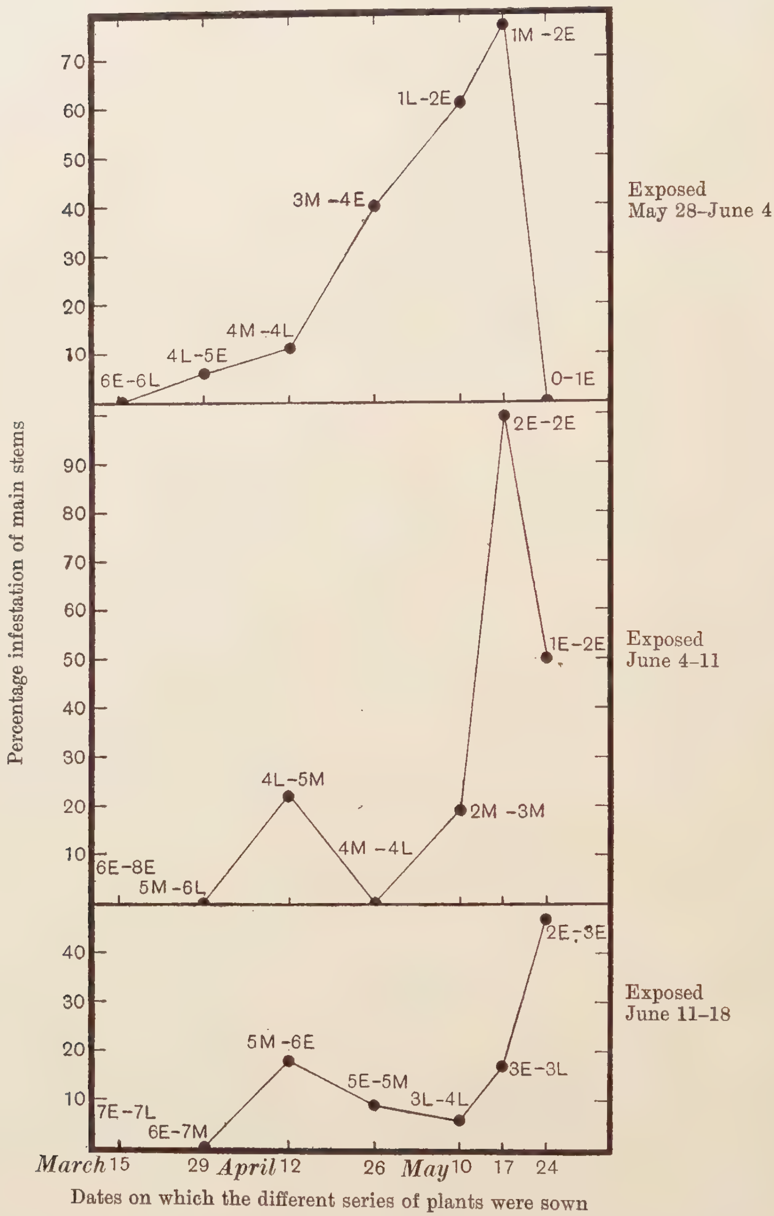


Chart 1. *O. frit* Linn. Infestations resulting from exposures made at Harpenden, 1923.

The first useful exposure (May 28--June 4) indicated that the main stem was highly susceptible while in the one- and two-leaf stages, much less so in the three- to four-leaf stages, and markedly less susceptible in the five-leaf stage and subsequent stages. The absence of infestation in the series sown on May 24th, when the plants on exposure were in the early single-leaf stage (having just appeared above ground) may have been due to either absence of susceptibility or absence of fly during the short time these plants were exposed to attack.

The next exposure (June 4–11) corroborated these observations to a great extent and indicated that the two-leaf stage was most susceptible, while the one-leaf stage was markedly less susceptible. The series sown on May 10th must be considered aberrant in view of the other observations and no explanation can be suggested for this particular case of low infestation of plants in the two-leaf stage.

The last exposure (June 11–18) was confirmatory of the previous exposures.

Experiment II. Oxford, 1923. *Chart* 2.

In this experiment, seeds of *Scotch Victory* oats were sown at the rate of eight grammes per six feet of drill, the drills being nine inches

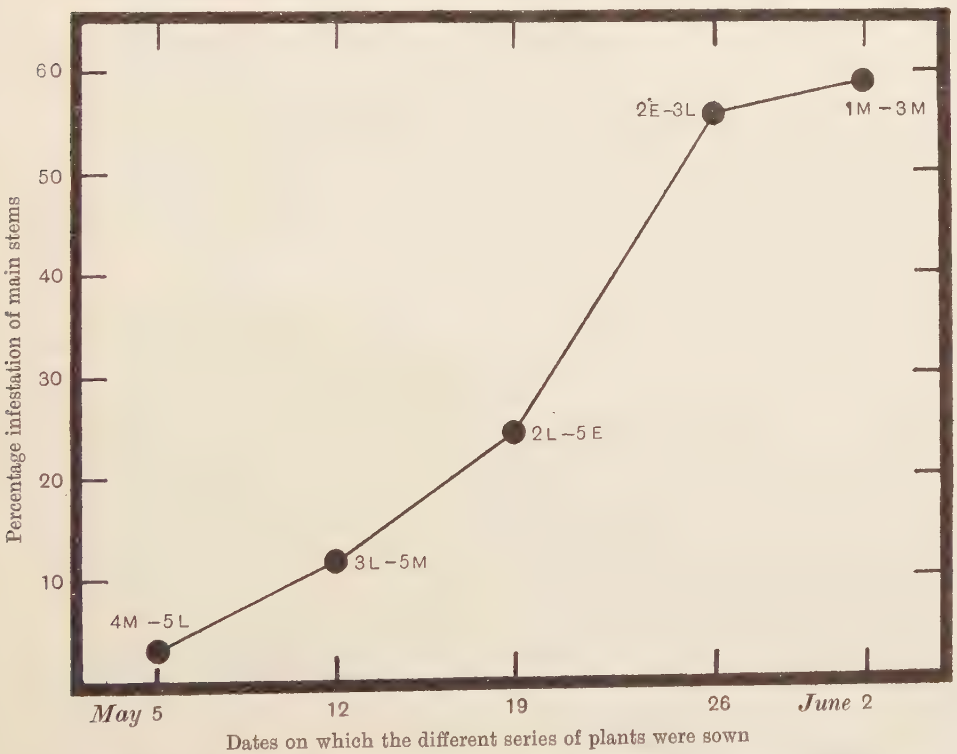


Chart 2. *O. frit* Linn. Infestations resulting from exposures made at Oxford, 1923.

apart and running north and south. The first sowing was made on May 23rd and followed by four more, at seven-day intervals. Reckoning from May 23rd, the plants appeared above ground after 7, 17, 21, 29, and 34 days respectively. During growth the plants were shielded from the fly by a muslin-covered cage, of dimensions 6 × 6 × 4 feet, which was removed on the 36th day and replaced on the 50th day. The exposure period was prolonged from 7 to 14 days because oviposition appeared to be very slight during the first seven days. The numbers of plants in the drills were, in order of sowing, 126, 119, 127, 118 and 115, respectively.

The data resulting from this experiment are shown in Chart 2. The two youngest series of plants during exposure passed from the medium one-leaf to the medium three-leaf stage and from the early two-leaf to the late three-leaf stage respectively and agree with the Harpenden plants (*vide* Expt. I) in being least immune. The next series passed from the late two-leaf to the early five-leaf stage and its immunity was decidedly increased. The two oldest series of plants (leaf formation during exposure—3 L to 5 M and 4 M to 5 L respectively) suffered light infestation only.

Experiment III. Oxford and Harpenden, 1924. *Chart* 3.

The experiment was approximately the same in the two localities. The experimental procedure was a repetition of that adopted for the Oxford experiment in 1923, except that conditions inside the cages were less abnormal because Frit Fly proof wire gauze was used for the cage coverings, in place of muslin. During this year growth was slow and consequently the first sowing was not made sufficiently early to obtain the range of growth required to demonstrate conclusively the immunity of the older plants.

Seed of *Abundance* oats was sown at the rate of 7·6 grammes per six feet of drill (Harpenden 4 grammes), the drills being nine inches apart and running north and south. Cover drills were sown where necessary and end plants were discarded when the plants were collected. At Oxford, three cages each 6 × 6 × 4 feet were used for covering purposes, while at Harpenden a number of small cages (2 × 2 × 3 feet) were available for the purpose. Sowing was commenced on April 23rd, subsequent sowings being made after 7, 14, 21, and 28 days reckoned from the above date. An additional drill was sown on the 35th day at Harpenden. The plants appeared above ground after 11, 19, 23, 26, and 34 days respectively in the order of sowing, again as reckoned from April 23rd.

The plants were exposed in three series, each series comprising

portions of each "age" drill; the first exposure was made from the 21st to the 28th day (May 14–21), the second from the 28th to the 35th day (May 21–28), and the third from the 35th to the 42nd day (May 28–

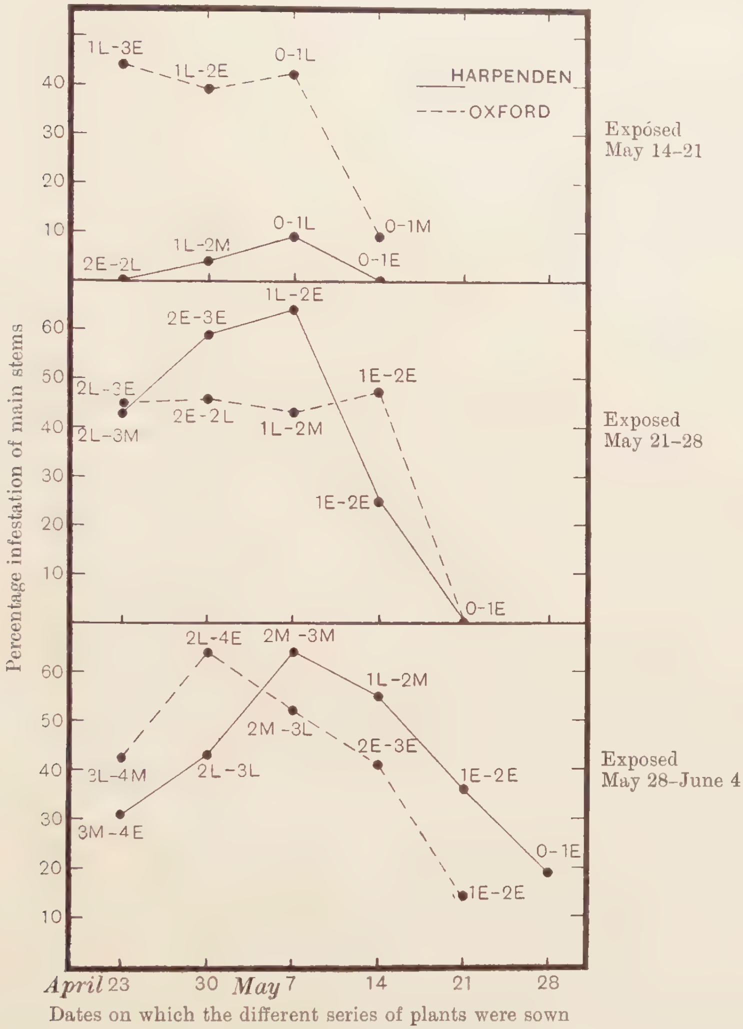
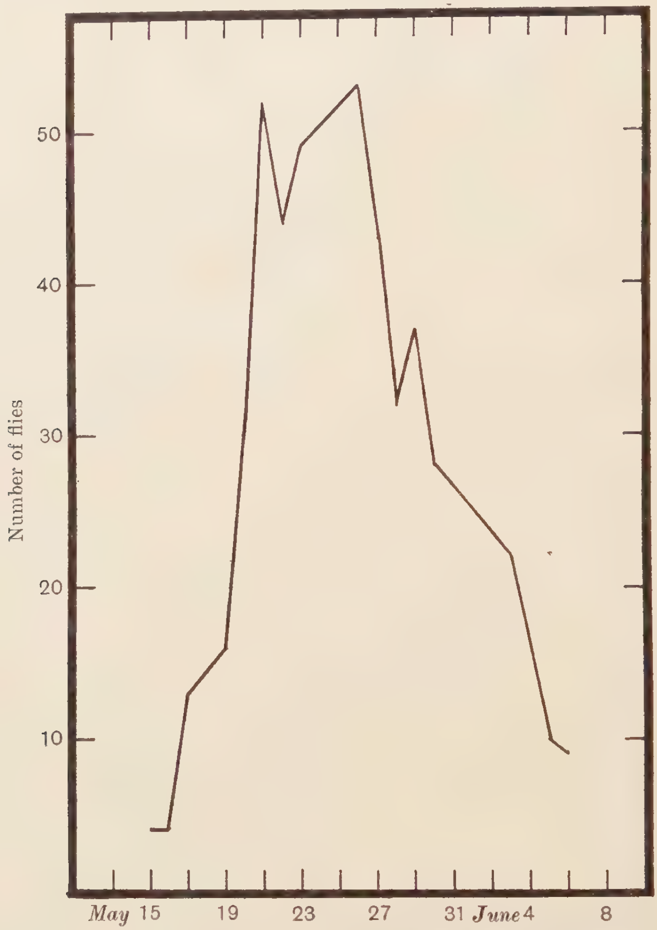


Chart 3. *O. frit* Linn. Infestations resulting from exposures made at Harpenden and Oxford, 1924.

June 4), the middle period (May 21–28) being arranged between these dates because of the apparent constancy of the prevalence periods of the fly (2). Rough determinations of the prevalence of the fly in the

field at Harpenden were made by the sweeping method, the fly being most abundant during the period May 21st to May 26th (*vide* Graph 1).

The minimum, mean, and maximum numbers of plants of similar growth exposed at one time were (*a*) *Oxford*, 99, 142, 158, and (*b*) *Harpen-*



Graph 1. *O. frit* Linn. Prevalence of the Frit Fly in the field at Harpenden during May, 1924.

den, 11, 28, and 47 respectively. Each series of plants, after exposure, was allowed fourteen days for the infestation to develop before examination. The percentage infestation, of the main stems of the plants of each series, incurred during each exposure is shown in Chart 3, together with

the changes undergone by the plants during exposure, as delineated by the change in the numbers of leaves borne by the plants.

First Exposure, May 14–21. As this exposure was made during the period 21–28 days after April 23rd, only the plants from the first two sowings were subject to infestation for the whole period. Those from the third and fourth sowings appeared above ground during the period (drill three on the 23rd day and drill four on the 26th day) and all the plants were in either the one- or two-leaf stage during exposure.

At Harpenden the infestation was practically nil (drill 2, 4·2 per cent., and drill 3, 9·4 per cent.), apparently owing to the scarcity of flies (*vide* Graph 1). At Oxford the infestation was equal where chance of infestation was also equal. The low infestation of the fourth series in this case again may have been due to the shortness of its exposure period.

Second Exposure, May 21–28. This exposure was made from 28 to 35 days after April 23rd and the fifth series of plants only appeared above ground the day before the replacement of the cage, hence the low infestation. Otherwise the result of the Oxford experiment, namely equal infestation throughout, was in agreement with previous results, all the plants being in the one- or two-leaf stage throughout the exposure. There is no apparent reason why the Harpenden curve should have shown a maximum about the series sown on May 7th, unless the variation was due to the smallness of the plant population.

Third Exposure, May 28th–*June* 4th[1]. All the plants of this series were above ground at the commencement of the exposure period, except the Harpenden drill No. 6 which was sown on the 35th day. From these exposures it would seem that very young plants were not, as one might have expected, highly susceptible to attack, that the two-leaf and three-leaf stages were most susceptible, and that immunity increased after the four-leaf stage was reached.

The two curves are remarkably similar in form, but the lag at Oxford is not in agreement with the plant development.

Summary.

Oat plants, of known stage of growth, were exposed to Frit Fly attack at different growth periods, with the result that the susceptibility of the main stem to attack was found to be most marked during the two- and three-leaf stages of growth. In the four-leaf stage susceptibility decreased and beyond this stage the shoot seemed to be immune relatively. Plants

[1] The coefficient of correlation between percentage infestation of main stem and tillering capacity, within this strictly limited period, was extremely high ($r = +0{\cdot}915 \pm 0{\cdot}046$).

in the early one-leaf stage showed a certain degree of immunity, due probably to size non-attractiveness rather than to specific morphological characters.

Considered in conjunction with the constancy of the prevalence periods of the fly, these observations have a certain importance. Thus a practical solution of the Frit Fly problem may be found either by early sowing (as is already well known) or by the selection of a variety which passes rapidly through all stages of growth preceding that described as the "four-leaved." The next step in the investigation would appear to be an examination of the different races or varieties of oat, in order to compare their rates of growth up to and including this stage.

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STUDIES ON *OSCINELLA FRIT* LINN. A NOTE ON THE SEASONAL REGULARITY OF THE MAXIMUM PREVALENCE PERIODS OF THE FLY IN THE FIELD

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(With 1 Chart.)

It has been suggested[1] that the frit fly appears in the field fairly constantly in time from season to season and that the normal population curve for the more southerly counties is of the type shown in the chart for the year 1922, these conclusions having been based on field and experimental observations made near Oxford during the period 1919 to 1922.

Corroborative data, which are considered to be of sufficient interest to merit being recorded, even although they do not form complete seasonal records, have been collected since 1922. In 1923 observations were made on oats purposely sown late in the season, namely on May 14th, near Oxford; the crop averaged about 1 inch in height by May 29th. By the courtesy of Mr J. C. F. Fryer, Director of the Pathological Laboratory (Ministry of Agriculture and Fisheries), Harpenden, it has been possible to compare some data relative to the changes in the frit fly population at Harpenden, during the year 1924, with the Oxford data recorded in previous years.

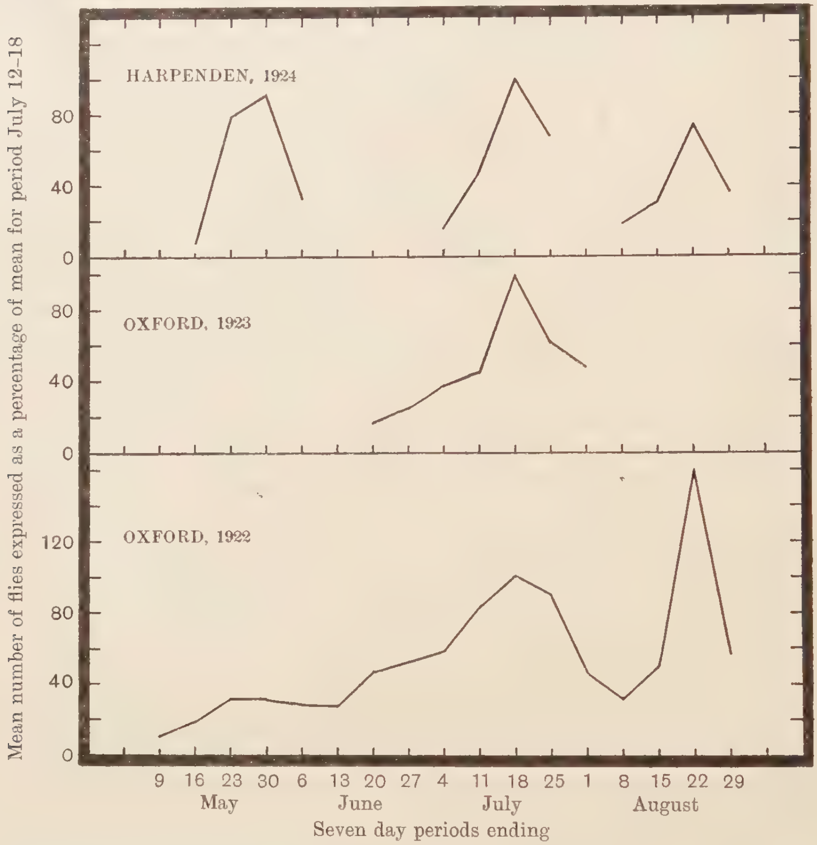
The methods of observation and graphical presentation of data have been described previously[1] and need not be recapitulated in this note. In the accompanying chart the records for the years 1922 to 1924 are shown as percentages of the respective mean observations for the seven-day periods ending July 18th.

During 1923, at Oxford, the oats appeared above ground just about the period of maximum fly prevalence as previously determined (May 26th) and, as shown on the chart, the intermediate generation again reached a maximum within the period ending July 18th. The maximum number of flies in the series (120) was actually recorded on July 13th. The commencement of this curve must represent immigrant flies and whether or no all the flies associated with the maximum were bred on

[1] Cunliffe, N. (1924). Further observations on the prevalence and habits of *Oscinella frit* Linn. *Ann. App. Biol.* XI, 54–72.

the oats or on wild host plants is immaterial, the important point being the appearance of the maximum within the period ending July 18th.

During 1924 sweeping at Harpenden was only conducted round about the maximum prevalence periods as determined at Oxford during previous years, and it should not therefore be inferred from the discontinuity of the curve that the fly is absent from the field during the intervening periods. Maximum records for the successive generations



were actually observed on May 26th (53), July 16th (82) and August 20th (55) respectively, and were entirely in agreement with previous records of dates of maxima.

Comparison of these curves shows that the periods of maximum prevalence do appear to be in remarkably close agreement from season to season, and it is this feature which it is desired to emphasise in this note.

(*Received May* 15*th*, 1925.)

INSECTS ATTACKING POTATOES IN NORTH WALES

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Observations on the insect pests of potatoes were commenced in a small way during the summer of 1921, crops being examined at several places, chiefly between Aber and Rhyl, as part of the general pest survey; it is of interest that in none of these were any aphides noted. In 1922 the work was more detailed, and a number of records were obtained.

In view of the importance of virus diseases, and the increasing recognition of the part played by insects as transmitters, and also considering the work in connection with these diseases being carried on at Bangor, it seemed advisable to obtain definite data. During 1923 a very considerable survey was attempted, and this was continued in 1924, when the work done was less widespread, but more detailed.

In all, some 200 different stations (fields, gardens, etc.) have been examined in the four counties of North Wales, but chiefly in Anglesey and Carnarvon. These observations have involved the examination of not less than 3000 plants at elevations varying from sea-level to over 1000 feet, and in all types of environment. Most of the records refer to attack upon the haulm.

Bourletiella lutea (Lubbock).

This minute yellow springtail is one of the most abundant potato insects in North Wales. In 1922 a few were present on the College Farm at Aber, and also on the mountain experimental plot on July 12th. In 1923 this insect was recorded at 15 out of 72 stations for which detailed notes were made. First noted on May 4th, it was very abundant in several places, reaching numbers estimated at 600 per plant on Sharpe's Express on a sheltered border in the College Farm garden, Aber, during May. This is the heaviest infestation seen anywhere as yet, but no marked damage was observable. It should be noted, however, that the insects were very small in size. Theobald (1) records several cases of severe damage to foliage in Kent during 1909, and figures the injury. In 1923 few were seen after the end of June.

In 1924 first records were obtained on May 27th in Anglesey. Although widely distributed it was nowhere abundant, although it occurred on the Mountain plot at Aber on August 11th, 1924, in numbers ranging from 2 to 10 on 9 out of 10 plants examined. These little creatures almost invariably occur on the under surfaces of the leaves.

B. hortensis (Fitch) = *pruniosus.*

This small dark species occurred two or three times during 1923, and also in 1924, but nowhere commonly, although widely distributed. It was present in fair numbers in a garden near Criccieth, June 19th, 1924, and near Mostyn on the 26th of the same month.

Onychiurus (*Lipura*) *ambulus* (L.).

On several occasions this species has been recorded as attacking potato tubers, chiefly those already damaged or rotting through fungoid attack. It is abundant, especially in wet seasons, and has caused serious injury to various garden plants in Carnarvonshire.

Achroutes purpurescens Lubbock.

One record of this on a diseased tuber, March 15th, 1922.

Aphides.

These have shown a progressive increase in numbers during the period of observation. But few notes were made during the hot dry summer of 1921, and no aphides were recorded, nevertheless, the stations examined included the College Farm, Aber, and several others along the coast to Rhyl. In 1922 they were present in small numbers, more particularly in the Bangor—Rhyl area.

In 1923 they were found in 47 out of 72 examinations at different places, whilst in 1924 they were seen still more abundantly, more especially Bangor—Llandudno Junction district. These years have all been increasingly wet and sunless. This abundance about Bangor in 1924 was not accompanied by a general increase, rather the reverse was the case. Some quite heavy infestations were recorded at Aber, even under conditions not especially favourable. From the observations made to date, and speaking broadly, there can be no doubt but that shelter plays a very important part in aphid infestations of potatoes. Almost all the higher counts have been obtained from sheltered fields and gardens, and especially in walled gardens where very early crops can be raised, and where early infestation resulted from glasshouses and frames, or shrubs, etc., on which the aphides may have over-wintered.

This latter question has not yet been fully cleared up, and is still under observation; several observations are recorded under the various species.

Macrosiphum solanifolii Ashmead.

This is by far the most abundant species on potatoes in North Wales, and such was markedly the case in 1924, especially on the College Farm. It has been obtained also from roses at Llanidan, Anglesey, on a wall, March 14th, 1923; and near Hawarden, June 11th, 1923; tomatoes under glass, Glan Conway, March 14th, 1923; and tulips (glass), Conway, March 15th, 1923.

In 1923, out of 72 localities this species occurred on potatoes in 29. Theobald (2) records this species from *Sonchus, Lactuca, Chenopodium,* Brassicas and others. In the U.S.A. Patch (3) records it from a very wide range of host plants and recommends the removal of rose bushes from potato districts.

Macrosiphum pseudosolani Theobald.

So far this species has only been found in limited numbers in 1922 and 1923. In 1922 it was recorded twice, once on haulm under glass, Bangor, May 1st, 1922, and once in a field near Conway, where apterous females were found in considerable numbers within the stamens of flowers of Majestic, August 17th, 1922. A few were also found on the leaves. In 1923 an interesting record was obtained in a garden at Llanfairfechan on March 7th, when a number of viviparous females and larvae were found on a number of "volunteer" potato plants growing among a bed of sprouting broccoli in a very sheltered field. Two females also occurred on loganberry shoots in a garden at Aber, March 6th, 1922. The winter of 1922–3 was exceptionally mild. In 1924 the species was not obtained.

Myzus persicae Sulzer.

This is an abundant species, with a very wide range of host plants. In 1923 it occurred in 23 out of 72 localities examined, and also under glass. In 1924 it was much less abundant. It has also occurred as a serious pest of sprouting potatoes, and in 1922–3 experiments on their control were carried out (4) at Bangor.

In addition to potatoes, it has occurred in North Wales on the following hosts: (*a*) under glass, Carnations, Chrysanthemums, Tomato, Smilax, Peach, Lilies and *Brugmannia*; (*b*) out of doors, Swede, Clover, *Lycium barbarum*, "Honesty," Jack by the Hedge (*Alliaria officinalis*), Red Valerian, Chervil, Violas and Lilies.

Aphis solanina Passerini.

Rather a scarce species. It was present with *M. solanifolii* on potato flowers at Conway, August 17th, 1922, and in small numbers on the experimental plots on the College Farm, Aber, August 15th, 1922. In 1923 it again occurred at Aber in some numbers during August, whilst in 1924 the only records were at Pentre Voelas, August 5th, 1924, at 850 feet, when very few were collected. It will be noted that all these records are in August. As stated by Theobald(2), "it occurs in the apterous stage under the leaves, usually in small scattered groups and closely applied to a vein." Theobald also states that it is not at all common and that very few alate females have so far been found. No alatae have yet been seen in North Wales.

It may be of interest to give here some figures regarding actual cases in which individual potato plants were examined *in situ*, leaf by leaf. (I) College Farm field trials, August 1st, 1923: 20 plants were examined at the centre of about four acres; growth dense, situation open and exposed. No living aphides were found on eight plants; the remainder gave the following counts: 1 apt. ♀ *solanifolii*; 1 apt. ♀ *solanifolii* and 4 larvae; 1 alate ♀ *persicae* and 1 larva; numerous larvae of *persicae* (and several dead ♀♀, sp. ?); several dead apt. ♀♀; 1 dead alate ♀ *persicae*; 1 apt. ♀ *solanifolii*; 1 larva, sp. ?; 1 apt. ♀ *solanifolii*; 3 ♀♀ and many larvae, sp. ?; 1 ♀ *solanifolii* and 2 dead apt. ♀♀. Dead aphides were common throughout the plot, both parasites and fungoid diseases being abundant. (II) On Arran Comrade, in a very sheltered situation in the garden, August 1st, 1923, ten plants gave the following counts: (1) none; (2) 5 larvae *persicae*; (3) 2 larvae *solanifolii*; (4) 10 apt. ♀♀ *solanifolii* and several dead specimens; (5) 8 apt. ♀♀ *solanifolii* and several dead; (6) 12 apt. ♀♀ *solanifolii* and several dead; (7) 10 apt. ♀♀ *solanifolii* and 10 dead; (8) 6 apt. ♀♀ *solanifolii*; (9) 20 ♀♀ *solanifolii*; (10) 5 *solanina* apt. ♀♀. Other counts were similar. Ten plants in another part of the garden yielded 55 *A. solanina* and 10 *M. solanifolii*. In 1924 the first record on potato was on May 29th, when 2 alatae of *M. persicae* were taken from 20 plants of Witch Hill, examined in a sheltered garden near Llandudno Junction, close to glasshouses and shrubs. In another garden (on the same date) *persicae* and *solanifolii* were present on Sharpe's Express; in this case apterous viviparous females, with some larvae. Twenty plants in an open field near by were free.

On 25 plants in a very sheltered garden near Nevin, June 20th, 1924, only 1 larva of *solanifolii* could be found; in a garden near Criccieth, on

the 19th, *solanifolii* was common, while in open exposed fields near the sea none were found. At Madryn Castle no aphides were recorded. In a very sheltered farm garden at Bottwnog numerous apt. viv. ♀♀ of *solanifolii* and a few larvae occurred, June 20th, 1924; and in a field near Aberdaron only 2 apterae of *solanifolii* were taken.

At Mostyn, in a sheltered garden, June 26th, 10 plants of Snowdrop yielded 26 apt. viv. ♀♀ of *solanifolii*, and numerous larvae, and 1 ♀ of *persicae*. On the College Farm, Aber, the following counts were made in Cae Cwrtiau field, July 23rd, 1924. It should be mentioned that accurate enumeration was difficult, as the plants were large, and a few aphides may have fallen, or been overlooked. The counts therefore may be taken to show minimum numbers. (1) 63 *M. solanifolii* (1 alate); (2) 96 *M. solanifolii* (2 alate, but the majority larvae); (3) 35 *solanifolii* and 1 alate *persicae*; (4) 40 *solanifolii* (1 alate); (5) 35 *solanifolii*.

In the garden at Aber, same date, four plants of Up to Date yielded: (1) 35 *M. solanifolii* (several dead and parasitised); (2) 75 *solanifolii*; (3) 90 *solanifolii* (and 1 *A. rumicis*); (4) 130 *solanifolii* and 1 alate *persicae*.

The crop was dense and formed a complete cover, meeting between the rows. For contrast ten plants of Kerr's Pink from the same bed were then examined. In this case the plant habit was very different, the haulm being tall and upstanding, leaving a clear space between the rows. (1) 1 apt. ♀ *solanifolii* (parasitised); (2) none; (3) 1 nymph *solanifolii* and several dead from fungoid attack; (4) 1 larva *solanifolii*; (5) 1 apt. viv. ♀ *solanifolii*; (6) 1 alate ♀ *solanifolii*; (7) 1 larva *persicae*; (8) 1 alate ♀ and 1 larva *persicae*; (9) 1 alate ♀, 1 apt. ♀ and 4 larvae *solanifolii* (also 1 dead larva, sp. ?); (10) 3 apt. viv. ♀♀ *solanifolii*. Further counts were made in the field called Bryn gwylan pellaf, at Aber, on July 24th. Two plants under the shelter of the hedge, cover dense but not complete, variety Tinwald Perfection (farm stock), gave (1) 70 *solanifolii*; (2) 23 *solanifolii* and 2 alate ♀♀ *persicae*. Six rows further out from the hedge five more counts produced: (1) 60 *solanifolii* and 1 alate ♀ *persicae* (also several dead aphides)—this was an exceptionally large plant; (2) 17 *solanifolii* and 1 alate *persicae*—this was a very small plant; (3) 70 *solanifolii* (and several dead); (4) 32 *solanifolii*; (5) 64 *solanifolii* and 2 alatae of *persicae* (several dead specimens). These three plants were ordinary well-grown examples. Two plants in mid field, where the growth was dense, yielded: (1) 64 *solanifolii*; (2) 65 *solanifolii*. None were alate, and several dead were noted.

Practically all aphides occur on the under surface of the leaves. A few Syrphid larvae have been noted here and there.

Near Conway, July 29th, 1924, *M. solanifolii* was fairly common in a sheltered field. At Holyhead, August 1st, 1924, a few specimens of *M. persicae* were present on badly blighted haulms. At Pentre Voelas, in Denbighshire, August 5th, 1924, in an open field at an elevation of 850 feet, ten plants of Kerr's Pink yielded 1 ♀ *solanifolii* (alate) and 1 apt. *A. solanina*. On the adjoining farm and in a very exposed field seven plants of Kerr's Pink gave 15 aphides (4 apt. viv. ♀♀ *persicae*, 10 *solanifolii* and 1 *solanina*).

On the mountain plots at Aber, August 4th, 1924, at 1000 feet, the following counts were made: (1) 2 *solanifolii* (1 apt. ♀ and 1 larva); (2) 6 apt. ♀♀ *solanifolii*, several larvae, and 1 dead ♀ sp. ?; (3) none; (4) none; (5) 1 dead apt. ♀ sp. ?; (6) 1 very small larva *solanifolii*; (7) 1 apt. ♀ *solanifolii*; (8) 1 apt. ♀ *solanifolii*; (9) 8 *solanifolii*; (10) 14 larvae of *solanifolii*.

Other aphides taken on potato were *Aphis rumicis*, which occurred several times, generally near mangolds, and in small numbers only. *Anuraphis pruni*, commonly, but merely migrating alatae from neighbouring plum trees. One or two other odd specimens of migrant forms may occur now and again.

Other Rhynchota were *Philoenus spumarius*, the Cuckoo Spit insect of which both young and adult examples were found here and there, especially on the mountain plots at Aber in July, 1922. *Chlorita* spp. are occasionally seen. *Psyllopsis* sp. probably *fraxinicola* occurred in small numbers in 1923 chiefly in the Vale of Clwyd. *Pseudococcus gahani*, a mealy bug, was discovered on sprouting potatoes at St Asaph in 1923. This appears to be a solitary record, and has been described elsewhere (5).

Plant bugs have been scarce, the only records of importance being *Calocoris norvegicus*, several at Aber, July 22nd, 1924, and a number at Conway, July 29th, 1924, and *C. sexguttulatus*, one specimen, July 22nd, 1924. Another small species (not yet identified) has been taken, but is rare. Among Coleoptera *Psylliodes affinis* is local, but may then be abundant. In 1923 it was present in sufficient numbers to cause considerable damage in two large gardens in Flint and Denbigh, and was present in smaller numbers in several others. In 1924 it was noted here and there, including Aber and near Nevin.

The larvae of the Chafers *Melolontha vulgaris* and *Phyllopertha horticola* occur on the roots and tubers now and again, but no really severe attack has been noted. Wireworms also cause damage.

I am indebted to Prof. F. V. Theobald, M.A., Dr G. H. Carpenter, Mr J. C. F. Fryer, M.A., and Mr R. Stenton, for the identification and verification of various insects[1].

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[1] A further considerable number of potato plants have been examined during the summer of 1925, in varying localities from sea level to 1000 ft. The summer has been of the hot dry type, and in marked contrast to 1923–24. There has been a notable diminution in the Aphis population, the numbers agreeing markedly with those noted in 1922. The chief cause for this change appears to be parasitisation of the apt. viv. ♀♀ during June, before colonisation could take place. Capsid bugs, however, showed a considerable increase, and haulm damaged by them was noted in a number of places. The species present were *Calocoris bipunctatus* (*norvegicus*), which was common; with *Lygus pabulinus* and *C. sexguttatus* less so. A few *Anthocoris* were seen, probably feeding on Aphides.

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NETTLEHEAD IN HOPS

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For many years a disease has been known in hops in Kent and Worcestershire under the name of "Nettlehead," "Nettly" or "Skinkly Hops," and in Sussex as "going silly." For the last 25 years this hop trouble has been frequently mentioned and remarked upon by growers and in places it has rapidly increased often to a very serious extent. Owing to this rapid increase an investigation into the cause and effect of "Nettlehead" disease was undertaken in the spring of 1914 and carried on till the summer of 1915, with the help of a grant from the Board of Agriculture and Fisheries. Unfortunately owing to military service a break of four years then occurred and the investigations were only renewed in June, 1919. Although a certain amount of interesting information had been gathered in 1914–15, it was found necessary to start almost afresh. Before any definite conclusions can possibly be arrived at as to the cause of the so-called Nettlehead, marked hills must be watched for at least consecutive summers. The notes here given are merely a record of observations and any suggestions are purely tentative. Although all unhealthy hills were termed "nettly," it soon became evident from a close study of the growth that there were two types of disease and only in one of these could the term "nettly" be truthfully applied. "False Nettlehead" has consequently been applied to the second form of disease. Only twice have the two forms of disease been found together in the same garden and in these instances cases of the "true" form far outnumbered the "false."

Characteristics of True Nettlehead.

Compared with a healthy hill a diseased plant is backward, lacks vigour, and usually makes fewer shoots. This cannot be laid down as infallible, however, as cases have come under notice where the hill appeared to be growing away well but instead of continuing this healthy growth it has suddenly ceased to grow, the leaves become "nettly" and the bine falls away from its support. Cases have also occurred where one bine only is "nettly," while the others are healthy and grow away.

In the case of this partial attack it is quite possible the hill will become completely diseased the following year when the attacking agent may have got a better hold upon the plant. In the case of a badly diseased plant the bine may be up to 5 feet in height; the leaves are small and generally lighter in colour than those of a healthy plant. Semi-transparent yellowish streaks occur along the ribs when the leaf is held up to the light, while the bine, instead of continuing to climb, invariably falls away from its support. The terminal leaves do not develop properly but remain in a semi-expanded or crumpled state.

True nettlehead has only been found in hills over three years old.

Characteristics of False Nettlehead.

The bine in this case usually attains the height of 5 feet in older hills, but in young hills it ceases to grow and usually dies when only a foot or so high. As in the case of true nettlehead, the leaves when fresh are in a crumpled state but are considerably larger and of a bluish colour; the internodes also are foreshortened, giving the plant a bunched-up appearance. In this case the bine does not fall away from its support, but after reaching a certain height the plant may either wilt and die away or remain fresh but in a dormant state. Six hills have been kept under observation and the bine measured weekly from May to August, but no growth took place after the middle of June and in four cases the bine was completely dead by August 16th. This wilting of the bine has been noticed at the end of May, but in the majority of cases it begins at the end of June and by August the foliage is quite dead and dry. The affection appears to spread through the whole "stock" and plant system. This form of disease has many times been found in quite young hills.

Loss and Conditions Favouring Appearance of Disease.

In the Weald of Kent particularly the loss caused by true nettlehead has been very considerable. Two gardens known to the writer were grubbed and the loss for three years on a third garden of eight years standing is estimated at £140.

False nettlehead is equally serious and the spread of the disease equally rapid. In 7 rows comprising 266 hills, 10 hills were grubbed in 1911; 28 hills in 1912; 44 in 1913; and 43 in 1914.

The grubbing of affected hills directly the disease made its appearance was found to be no safeguard. Owing to the short period covered by this investigation it has been found impossible to determine the effect of weather on the spread of the disease. Gardens with the worst

attack of true nettlehead are usually found to slope down to a stream or hedge with large trees in it, the nettlehead appearing in those hills on the lowest part or nearest the ditch and spreading inwards, but this is not invariably the case. There is evidence that pasture land put down to hops commonly shows the disease in about the third year.

The districts in Kent which have come under observation are as follows: Wye (true and false), Cranbrook, Staplehurst, Goudhurst, Sissinghurst and Sittingbourne (true), Chilham (false). In Worcestershire the true form of the disease was particularly bad at Suckley in 1912. A few cases of false nettlehead were also noted.

Cause of Disease.

It has hitherto been supposed that an eelworm—*Heterodera Schachtii*—is the cause of the disease. Percival (1) was the first to discover this Beet eelworm in connection with diseased plants and since that date (1895) no further research has been carried on until the present investigations were begun. As a result of these a doubt is now cast on the theory that eelworms are responsible.

Examination of the rootlets of both diseased and healthy hills has revealed the female eelworm often in considerable quantity. Unlike the majority of the Anguillulidae, the genus to which this eelworm belongs is dormant in the female stage and in the case of the eelworm under discussion may be found, especially in the winter months, adhering to the fine fibrous roots as a brown citron-shaped body, clearly visible to the naked eye though only from 0·45 to 0·725 mm. in length. In the case of the other genera the sexes are both eel-like and found in masses in the plant tissues so that it would be quite impossible to count the numbers with any accuracy. The peculiar form of the female *H. Schachtii*, however, enables the number upon any one rootlet to be gauged with some degree of accuracy. As with only one exception the eelworm has been found upon the fibrous roots of all varieties of hops, the name of the variety is omitted in the following tables. The exception is the Foundling and figures relating to this will be found in Table IV.

It might appear from a comparison in Table V that a hill can withstand the ravages of a certain number of eelworms, but when the number increases upon the rootlet the disease will appear. Up to the present there is not sufficient evidence to state this definitely. However it may be advanced against this theory that many perfectly healthy hills were examined in 1919 showing a considerable number of eelworms

(Table VI). It was thought at first that the Foundling might be immune but two cases of true nettlehead were recorded in 1915 on this variety.

In February, 1915, a garden (*A*, Table VII) was examined which had been grubbed in 1903 and replanted with Fuggles, one half in 1911 and

Table I.

Examination of the rootlets of twelve "hills" showing True Nettlehead.

Place	Number of female worms	Length of rootlet	1 eelworm to
Suckley, Worc.	37	176 ins.	4·7 ins.
,, ,,	174	428	2·4
,, ,,	143	333	2·3
,, ,,	24	139	5·7
,, ,,	35	287	8·2
,, ,,	31	247	7·9
Wye, Kent	94	326	3·45
,, ,,	30	218	7·2
,, ,,	22	68	3·09
,, ,,	5	60	12·0
,, ,,	6	75	12·5
,, ,,	24	116	4·8
	625	2473	3·9

Table II.

Examination of sixteen hills attacked with False Nettlehead.

Place	Number of eelworms	Length of rootlet	1 eelworm to
Wye, Kent	1	111 ins.	111 ins.
,, ,,	0	Root decayed	—
,, ,,	0	,, ,,	—
,, ,,	0	,, ,,	—
,, ,,	0	,, ,,	—
,, ,,	0	,, ,,	—
,, ,,	0	,, ,,	—
,, ,,	0	,, ,,	—
,, ,,	0	,, ,,	—
Chilham, Kent	0	112 ins.	112 ins.
,, ,,	0	Decayed	—
,, ,,	0	,,	—
,, ,,	0	,,	—
,, ,,	0	,,	—
,, ,,	0	,,	—
,, ,,	0	25 ins.	25 ins.
	1	248 ins.	248 ins.

In thirteen hills the rootlets had decayed away and in the remaining three the rootlets were dead.

Table III.

Examination of rootlets of healthy hills.

Place	Number of eelworms	Length of rootlet	1 eelworm to
Suckley, Worc.	29	693 ins.	23·5 ins.
,, ,,	0	455	—
,, ,,	76	457	6·01
Wye, Kent	138	789	5·7
,, ,,	186	1114	5·4
,, ,,	20	340	17·0
,, ,,	95	353	3·7
,, ,,	6	284	47·3
,, ,,	0	128	—
,, ,,	0	186	—
,, ,,	1	132	132·0
,, ,,	155	1174	7·5
,, ,,	173	527	3·04
,, ,,	220	590	2·7
,, ,,	1	119	119·0
Cranbrook, Kent	75	412	5·3
,, ,,	50	425	8·5
,, ,,	57	465	8·1
Goudhurst, Kent	196	623	3·1
,, ,,	119	660	5·5
,, ,,	83	734	8·8
Wye, Kent	32	873	27·2
,, ,,	22	452	20·5
,, ,,	44	505	11·4
,, ,,	51	504	9·8
,, ,,	72	678	9·4
,, ,,	51	1270	24·9
,, ,,	110	1091	9·9
,, ,,	46	763	16·5
Chilham, Kent	59	1004	17·01
,, ,,	114	1143	10·02
,, ,,	81	1352	16·70
	2362	20,495	8·6

Table IV.

"Foundling."

A variety at first thought to be immune and having a high percentage of eelworm, at the same time showing no signs of disease.

Place	Number of eelworms	Length of rootlet	1 eelworm to
Wye, Kent	237	467 ins.	1·9 ins.
,, ,,	628	1011	1·6
,, ,,	150	400	2·6
,, ,,	69	163	2·3
	1084	2041	1·8

Table V.

Summary of Tables I, II, III and IV. Giving a comparison of True, False, Healthy and Foundling Hops.

Table	No. of hills examined	Nature of hill	No. of eelworms	Length of rootlet	1 eelworm to
I	12	True nettlehead	625	2,473 ins.	3·9 ins.
II	16	False nettlehead	1	248	248·0
III	29	Healthy	1362	19,295	14·3
IV	4	Healthy (Foundling)	1084	2,041	1·8

Table VI.

Showing the number of eelworms found on healthy plant roots.

Place	Number of eelworms	Length of rootlets	1 eelworm to
Suckley	43	158 ins.	3·6 ins.
,,	46	186	4·04
,,	40	130	3·2
,,	246	564	2·2
,,	591	900	1·5
,,	102	280	2·7
,,	121	335	2·9
,,	158	338	2·3
	1347	2911	2·2

the other in 1912. The rootlets from 70 hills were grubbed and carefully searched for eelworm, but no citron-shaped females could be found. In July, 1919, this garden was again visited and 32 hills examined. Of these, 19 hills were entirely free from eelworm, while the remaining 13 yielded large numbers. This garden which slopes down to an alder-covered stream, has seemingly all the requirements for the appearance of the disease, but nettlehead has not been present there during its six years' existence.

In a garden (*C*, Table VII) one half (x) had been planted up in 1911, while the other (y) was planted in 1912; an examination was made in February, 1915, and again in June, 1915, when several hills were seen to be slightly diseased. A re-examination in July, 1919, showed the increase of eelworm in this garden to have been considerable, the rootlets in some cases being completely covered with the creatures, but no disease was noticeable in any of the hills.

In a third case (*B*, Table VII), a garden which showed signs of the disease in many hills was practically free from eelworm in June, 1915, whereas in 1919 there was a considerable increase in the nematode but

the disease had vanished, those hills which showed signs in the summer of 1915 having been grubbed.

A comparative table of these gardens is appended.

Table VII.

Showing decrease of disease but increase in numbers of eelworms.

Garden	Year	Length of rootlets	Number of eelworm	Remarks
A	1915	11·571 ins.	0	Free from disease
A	1919	4·317	264	Free from disease
B	1915	5·000	9	Signs of disease
B	1919	1·832	389	Free from disease
C (*x*)	1915	5·178	1	Signs of disease
C (*x*)	1919	2·806	1001	Free from disease
C (*y*)	1915	5·000	0	Free from disease
C (*y*)	1919	0·839	192	Free from disease

Conclusion.

A study of Tables VI and VII shows that *H. Schachtii* is not the cause, or at all events the primary cause, of nettlehead disease. It seems unaccountable that hops planted up in newly-ploughed pasture land should become diseased with such regularity in certain districts; especially so when eelworm has not been found upon any weed which would be likely to harbour it in grass land. It has, however, been recorded by Theobald from Yorkshire on Oats and from Essex upon Peas, and Fryer records it from Wales upon Potato. No explanation is forthcoming for the fact that symptoms of the disease may be found in gardens with comparatively few eelworms, and that this disease dies out as the eelworm increases. It has been noticed that the disease has been much in evidence after a severe aphis attack and the writer puts forward the theory that the disease is carried not only by these insects but also by the knife in spring. There is no evidence to show that *H. Schachtii* is the primary cause of the disease.

Summary.

1. Under the name "Nettlehead" two quite distinct diseases, "true" and "false," have been noticed.

2. In the case of "False" Nettlehead the bine usually dies away in August and the root system is in a state of decay; in the "True" form the bine remains green though growth is retarded, at the same time the root system remains in an apparently healthy state.

3. The "True" form is usually to be found starting from the edge of a garden especially where the garden slopes down to a deep ditch or high hedge. "False" Nettlehead, on the other hand, may be found distributed throughout the garden.

4. The Beet eelworm, *Heterodera Schachtii*, may be found in all hop gardens, but its presence is not correlated with "Nettlehead."

5. "True" Nettlehead has been in greater evidence the year following a bad attack of aphis.

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REVIEWS

Imperial Botanical Conference. Report of Proceedings. Edited by F. T. Brooks. University Press, Cambridge, 1925.

International congresses of botany were held at Paris in 1900, Vienna in 1905 and Brussels in 1910. The fourth congress should have been held in London, but, in 1915, this was made impossible by the war, and, in 1920, by the peace. The best substitute was an Imperial Conference and this, the first of its kind, met in London in 1924. The viewpoints of people looking at botany imperially necessarily differ from those obtained when the same subject is seen internationally and doubtless had an International Congress met last year the programme and proceedings would not have resembled those of which the present volume is a report. If one compares this volume with the two volumes issued by the Brussels Congress in 1910, a great difference is apparent not only in the general format of the meeting but in the entire outlook of the conference.

Vol. I of the Brussels Report contains 373 pages, many devoted to general congress organisation and details, but the scientific sections are apportioned as follows: botanical nomenclature, 74 pages; phytogeography, 47 pages; bibliography and documentation, 151 pages; and teaching of botany, 34 pages. Vol. II contains papers read to the Congress, physiology occupying 12 pages, plant structure and evolution 6 pages, and systematic botany and ecology 216 pages. In the London Conference Report 30 pages are devoted to plant physiology, 73 to genetics, 92 to plant pathology and mycology, 105 to systematic botany and ecology, 7 to rules of nomenclature, 15 to education and research and 50 to papers mostly of a semi-economic character. The difference in the viewpoints and the balance of values in these two Reports does not merely reflect the difference between Imperial and International botanics; it reflects fundamental changes that have occurred in the science itself; new orientations of thought and striking developments that began to be noticeable in botanical research some 15 or 20 years ago. The active botanists of the nineteenth century were largely systematists and morphologists; the active botanists of the twentieth century are mostly plant pathologists, physiologists, geneticists, ecologists and economic botanists.

This change in outlook is very largely due to the fact that until about two decades ago botanical research in this, as in other countries, largely emanated from the academic schools of botany, but, to-day, it is probable that at least as much research comes from outside sources such as various government departments and research institutes. Of course, in certain cases, the latter are attached to universities, but even so, the research and teaching staffs often tend to remain distinct and, further, much of this extra-academic research is published in journals not usually found in academic libraries.

Discussing the Conference Report, more than one well-known teaching botanist has confessed to me that "I am a little lost" and that "this botany is not my botany." There are an increasing number of research workers at present outside academic botany, and in touch with perhaps a wider and more real field of plant life, who rather feel that the academic schools are very conservative and somewhat inbred institutions and that students are being reared in an atmosphere of scholasticism. To them the classical botany of the schools seems as though it is tending to occupy a position somewhat similar to the classical languages in philology. Such a volume as the Conference Report should act as a signpost in Botany indicating the distance travelled and directing the way of botanical scholiasts along more real paths. For the sake both of "their botany" and their students it behoves them to open their eyes to the live world about them, and to open their minds.

The volume is very sensibly produced but would have been much improved by a more detailed and synoptic "Contents." Like many other Conference Reports it

possesses no index—surely a cardinal sin. By most botanists the volume will always be treasured if only for its frontispiece, a fine portrait of a great-hearted and much loved man.

WM. B. BRIERLEY.

Laboratory Outlines in Plant Pathology. By H. H. WHETZEL, L. R. HESLER, C. T. GREGORY and W. H. RANKIN. Saunders, 1925.

This book, first published in 1916, is now issued in a second edition completely revised and rewritten by the senior author.

The classification of diseases into three groups is maintained but the old heading of "Metaplastic Diseases" has become "Hyperplastic Diseases." There are certain other changes in terminology, such as the deletion of the minor heading "Cause, not an organism," and in substitution thereof "Physiogenic Disease" to include Stippen of Apples and Edema, and "Caused by Viri" to include the Mosaic diseases. Other new terms and concepts are to be noted in the glossary, especially perhaps "suscept" as differentiated from the familiar "host," and all seem to be justifiable innovations. Eleven of the original exercises have been omitted and five new ones added. The individual exercises show considerable alteration much more attention being given in this edition to symptomatology. This is a move entirely in the right direction for Plant Pathology is still, to its very great hurt, dominated by systematic mycology, and any influence tending to a truer balance of values is welcome. The diseased plant which is the content of plant pathology presents as many aspects of study as the diseased animal and systematic mycology is just about as useful in plant pathology as systematic bacteriology is in veterinary medicine.

A great improvement in the exercises in the new edition is the continual reference to selected original papers and, if the student conscientiously works through the chosen examples following the advice given, he should, at the end of his course, possess a fairly good idea of the literature. Too many teachers fail to bring their students into effective contact with the stimulus of contemporary research and a great many graduates leave the academic schools possessing practically no knowledge or perspective of the modern literature of their subject.

The book, naturally, is written from an American standpoint, and certain of the diseases used for practical exercise are not found in this country, but, in spite of this, it is a volume that should be in the hands of every English student of plant disease.

There are more misprints than one likes to see in a book so well produced as this.

WM. B. BRIERLEY.

British Weeds. Their Identification and Control. By R. MORSE and R. PALMER. Benn, London, 1925. 10*s*. 6*d*.

This book, in its sub-title, is described as "a practical handbook for the use of estate owners, farmers, gardeners and students of agriculture, horticulture and field botany," and it is stated that "Our investigations and experiments began at least fifteen years ago, and have been worked at continuously in various parts of the country since that time. It is claimed that the book "is unique in at least five important features, namely: (1) The arrangement of the weeds in alphabetical order according to the habitats in which they are usually found. (2) The systematic and orderly description of each species, in non-technical language. (3) The provision of an original and simple key to the identification of the plants described, constructed expressly for the use of readers having no knowledge of botany. (4) The ease and simp.icity of reference secured by the alphabetical arrangement and the Indexes. (5) The comprehensive nature of the contents, and the most up-to-date methods of control."

For practical purposes, and the book does not pretend to any other, the alphabetical arrangement according to habitat is quite convenient. The descriptions of the several species are on the whole good, being brief, in simple language, and yet fairly

diagnostic. The notes on economic uses, control measures, etc., appended to each description are in most cases useful and to the point. The "original and simple key" to identification is apt to give a botanist shocks but it has been tried out on several plants by a non-botanist and found to work. "Students of agriculture, horticulture and field botany" will, however, be well advised to put this volume on one side and keep to the standard floras for their specific determinations.

There are some eight appendices dealing with various economic aspects of the weed problem and whilst some of these are useful others are very incomplete. Appendix 7 is headed "Some Books of Reference" and although books on Weeds have been published from time to time not one is mentioned in this appendix. H. C. Long's *Common Weeds of the Farm and Garden*, published in 1910, and W. E. Brenchley's *Weeds of Farm Land*, published in 1920[1], might both be regarded as better and more comprehensive works than the present volume and although this is a pleasant enough book it is really a little difficult to see why it has been written or to find in it any commensurate value for fifteen years' investigations and experiments.

WM. B. BRIERLEY.

Organic Adaptation to Environment. Edited by M. R. Thorpe. Yale University Press, 1924. 18*s*. net.

This volume, published by the Amasa Stone Mather Memorial Publication Fund, contains a series of lectures by various well-known workers delivered before the Palaeontology Club of Yale University. During the last ten years American biologists have produced a number of volumes of this nature dealing with the broader evolutionary problems and although many of these have been very interesting and useful, this perhaps is one of the best.

The symposium was organised with a view to obtain exact data on the question of Organic Adaptation, the subject being considered from the standpoint of biological and geological evidence. The chapter headings which show the wide scope and authoritative treatment of the problems are given below.

I. The Terrestrial Environment in its Relation to Plant Life, by G. E. Nichols. II. The Protozoa and the Problem of Adaptation, by L. L. Woodruffe. III. Environment as a Stabilising Factor, by A. Petrunkevitch. IV. Mutation and Environment, by W. R. Coe. V. Fossil Plants as Evidence for Resistance to Environment, by G. R. Wieland. VI. Phases of Cephalopod Adaptation, by C. O. Dunbar. VII. Dinosaurian Climatic Response, by R. S. Lull. VIII. Environment and Racial Character, by E. Huntingdon.

It is, here, hardly possible to do more than draw attention to the rich feast provided, for any criticisms on a book of this nature would necessarily be of detailed facts and issues in particular essays and, largely, of matters of personal interpretation. The work has of course no direct or immediate application to Economic Biology, but it is one of the most interesting and thoroughly worth-while volumes that I have read for a long period. The work is beautifully produced, sufficiently illustrated, free from misprints and concludes with a good index.

WM. B. BRIERLEY.

Statistical Methods for Research Workers. By R. A. Fisher. Pp. 239, with six tables. Published by Oliver and Boyd, 1925. 15*s*. net.

Up to some twelve years ago, numerical results from biological investigation were customarily presented without evidence of statistical significance. Mendelian experiments from 1900 onwards aroused keen interest in the precise significance of numbers and ratios. A critical attitude, especially towards yield trial figures, soon became general. Other advances followed. Statistical method was found to afford the biologist not merely checks on numerical reliability but also forms of analysis, of interpretation and of procedure. And now, universally, the elements of statistics are regarded as indispensable to the biologist.

[1] Quite the best volume on Weeds is *Ugress I Nutidens Jordbruk*, by Emil Korsmo, published in 1925.

Not everyone with an inclination to the study of living things is fitted to become a statistician. To some the fundamentals are never comprehensible: at the opposite extreme are the mathematically-minded who revel in normal curves, variance, sampling and all their companions and complications. But the average biologist occupies a rather struggling intermediate position. Perceiving that statistics can offer him manifold aid he strives to master the algebraic proofs in which its processes are founded. It is of him essentially the accomplished statistician should think in writing a manual for biological investigators.

"To put into the hands of research workers, and especially of biologists, the means of applying statistical tests accurately to numerical data accumulated in their own laboratories or available in the literature"—this, in its own words, is the book's prime object. The method employed is that of fully worked numerical examples. These, forty-six in number, make the bulk of the book. With such a method success must turn on the appropriateness of the explanatory passages. And here we confess to some disappointment. Even chapters embracing involved and often novel processes are ushered in by explanations comprehensible only to those already fairly familiar with the elements of statistics. Algebraic proofs of the formulae used in the examples are not given. It is suggested that "by a study of the processes exemplified the student should be able to ascertain to what questions in his own material such processes are able to give a definite answer." That this hope will be realised in the case of the biologist as yet untutored in routine statistical methods appears far from certain. To the whole-hearted biologist it is a fearsome thing to make extensive use of formulae of which he has not mastered the proofs. He feels, and not without reason, that imperfectly understood mathematics may take him where biology cannot follow. Insistence on proof before formula may partially tie his hands: but that may keep biological hands out of mathematical mischief. A "formula-mill" has often stimulated the collection of data and expanded the out-turn of results without assuring their biological significance.

To us the book presents itself as an advanced manual for the biologist with mathematical leanings. And to an investigator who has applied himself already to the elements of statistics and gained some experience of their applications, it offers a great deal. Its table of contents, made up of Distribution, Goodness of Fit, Significance, Correlation, and Analysis of Variance, does not reveal the distinguishing features. The comparatively simple customary methods biologists have learned to use—and often to use without discrimination—are fortified by modifications and some new procedures. Specially adapted treatment for every set of results is the distinguishing feature. The "infinitely large" sample never approached in practice but assumed in the derivation of widely used methods, is disrespectfully jostled by the tantalising but more real "small" sample. For this we are much indebted. Accounts of the χ^2 test of fit, with appropriate tables, and of the analysis of variance, make these important matters no longer inaccessible to the ordinary investigator. A marked flexibility and resourcefulness in examination and analysis will re-awake interest in those who have grown content with stereotyped methods.

That biologists should be solemnly warned by a statistician against the possible dangers of statistics is perhaps not to be asked. And yet the necessity for a warning is real. The inglorious career of the correlation coefficient in investigation is proof of this. Collection of data in order to determine a correlation with scarce an effort to place upon it any biological interpretation, may almost be reckoned as a modern research method. Not every statistical process to which numerical data can be submitted nor every elaboration of procedure statistical considerations suggest, is acceptable in practical investigation. To have exemplified this clearly would, from the point of view of biology, have added greatly to the value of the manual.

It may not be true to say that this new manual is precisely what the average biologist needs. But for the investigator determined to make statistics merely his tool, and anxious to employ it as extensively as with biological safety he may, the book is a store of information and stimulus.

F. L. ENGLEDOW.

OBITUARY

PROF. H. MAXWELL LEFROY, M.A.

Economic entomology suffered the loss of one of its leading English exponents in the death of Prof. Harold Maxwell Lefroy on October 14th last and his co-workers both at home and abroad will have learnt the news with feelings of genuine regret. For some time past Lefroy had been experimenting with various toxic gases with a view to discovering any which offered promise from the insecticidal standpoint. While carrying out this work he evidently subjected himself to serious risks and, up to the time of his death, he was suffering from the results of previous exposure to a gas of a highly poisonous character. On Saturday, October 10th, he was found lying unconscious on the floor of his laboratory at the Imperial College of Science and Technology where he was overcome by the noxious properties of a gas which he had been testing. This misadventure occurred in the evening when the College was practically empty and, although he was removed as speedily as possible to St George's Hospital, where oxygen and other treatment was administered, he never recovered consciousness and died four days later.

Born on January 20th, 1877, at Itchell Manor, Crundall, Hants., Lefroy was educated at Marlborough College and from there he entered King's College, Cambridge. He graduated in 1898, securing a first class in the Natural Sciences Tripos and a year later he was appointed entomologist to the Dept. of Agriculture for the West Indies. During his occupancy of this post Lefroy gained his first experience of dealing with insect pests under tropical conditions and in 1903 he obtained the important position of Imperial Entomologist to the Department of Agriculture for India. It was in this capacity that Lefroy had his full opportunity of exercising his undoubted abilities for organization and for dealing with big practical problems. At the Pusa Institute he succeeded in building up a most efficient department and staffed it with men trained under his own supervision. He was confronted on all sides with a multiplicity of problems which would have damped the ardour of any average individual, but not so with Lefroy, in fact the more work he undertook the more alive and enthusiastic he seemed to become. The difficulties which he had to surmount can only be fully appreciated by those who have undergone kindred experiences under tropical conditions. There is no doubt that India owes much to Lefroy's pioneer influence, since he not only laid the foundations of much valuable economic work, but he also gave his subject a definite status in the eyes of the Government, and he convinced officials over him of the vast toll insects were exacting in the reduction of the yield of the staple crops of the country. Although his tenure in India only lasted eight years, the number of memoirs and bulletins which bear his name, or those of his associates, affords ample testimony to what he accomplished. In that period he also issued his *Indian Insect Pests* and his better-known book *Indian Insect Life.*

Lefroy returned to England towards the end of 1910 and lectured for some months at the Imperial College of Science where in 1912 he was appointed its first professor of entomology. His eminently practical and lucid methods of teaching, coupled with his enthusiasm and his personal sympathy and generosity, will be remembered as a source of inspiration by many of his pupils who are now widely scattered in various parts of the British Empire. As a teacher he held very pronounced views. Entomology to him was a severely practical subject and the average zoological training of a typical English university made little appeal to him. He maintained that the student of economic entomology cannot devote much time to morphological accuracy —it matters, for example, more to him how mouth-parts function than what is the correct name for each part. Habits, life-histories and control measures were the key notes of his writings and teaching. His aim was to train men ready to go out and deal with problems in the field and for such a class of worker he had little belief in the value of elaborate scientific training or technique.

During the War Lefroy was attached to the Field Force in Mesopotamia with the temporary rank of Lieut.-Colonel. In this capacity he organized sanitary measures for controlling flies and kindred pests which were menacing the health of the troops. He was recalled to England later in order to deal with the immense stores of insect-infested grain which were awaiting opportunity for shipment in Australia. It was imperative to find some methods of freeing such material from insect attacks, in order to save it from utter ruination, at a time when shortage of food supplies was one of the most cogent factors in the world war. On arrival home he made a rapid survey of the problem and soon afterwards proceeded to the United States for the purpose of examining the large-scale methods in vogue for cleaning pest-ridden wheat. Thus armed, he continued his journey to Australia, where, in a remarkably short space of time, he sized up the whole problem and recommended practical measures for treating the vast accumulations of infested grain. On his return to this country, Lefroy resumed his teaching duties at the Imperial College and also devoted a good deal of time to insecticides, accumulating a mass of data much of which, however, was never published. These investigations led him into purely chemical work, and, at times, he appeared to carry out his experiments forgetful of the possibility of incurring personal danger or discomfort. The ravages of the Death Watch beetle, in the woodwork of ancient buildings, also attracted his notice and he devoted a good deal of attention to the insect in connection with the roof of Westminster Hall. In conjunction with a leading chemist, Lefroy was able to devise effective control measures and thereafter he was looked to for advice by those concerned with the preservation of ancient churches and other buildings.

A short time after the termination of the War Lefroy was requested to report to the Government of India on the possibilities of extending silk culture in that country. His recommendations, however, were not given effect to owing largely to a reversal of financial policy which rendered new development in that direction impossible.

Among his other activities Lefroy was honorary Curator of the insect house at the Zoological Society's Gardens and for three years he was secretary of the Association of Economic Biologists. He joined the latter society in 1904 and took the leading part in its reorganization but resigned his membership in 1920. Along with the present writer he launched the *Annals of Applied Biology*, a journal which he edited during the period he was secretary of the Association. He served the interests of the Society in the same energetic manner which characterized his other activities. He was genuinely anxious that the Association should exert such influence as it possessed in recognizing applied biology as a definite profession. With this aim in view, Lefroy fostered a scheme which involved the incorporation of the Association as an official examining body, following the example of the Institute of Chemistry. Most of his colleagues felt there were grave difficulties in carrying out such a proposal, and the matter ultimately fell through.

Lefroy was a fellow of the Entomological and Zoological Societies of London, but was only an occasional visitor at the meetings of the first-mentioned body. He was a stimulating public lecturer and occasionally delivered discourses at the Royal Institution. In character he was a man of restless and energetic temperament and gifted with great enthusiasm for any work he happened to be carrying out. Like other men of strong personality, Lefroy was at times in collision with people who held divergent views to his own, but those who knew him best, and understood him, found him too busy to maintain personal resentment.

Outside his entomological work, Lefroy was extremely active as a motorist. The pursuit appeared to provide his ardent spirit with an acceptable slice of adventure. As a driver he took frequent risks and often drove at what is regarded by most people as an uncommonly high speed. On more than one occasion the present writer has experienced somewhat unusual "thrills" while being driven by the professor through the London traffic.

Lefroy's death at the early age of forty-eight has deprived entomology of a striking personality and our sincere sympathy is extended to Mrs Lefroy and her son in their tragic bereavement.

A. D. IMMS.

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